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Vol. 164

Part 1

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1953

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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1951-52

Vol. 164

Part 1

PROCEEDINGS OF THE GENERAL MEETING ON 11 October 1951

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The PRESIDENT welcomed the presence at the Meeting of Dr. E. D. Merrill, F.M.L.S. and Professor Richard Biebl.

The Proceedings of the Anniversary Meeting held on Thursday, 24 May 1951, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Miss E. Godman, Dr. G. A. C. Herklots, Mr. R. H. Jeffers, Mr. Richard Morse, Professor J. Omer-Cooper, Professor T. G. B. Osborn, Dr. Hugh Scott, F.R.S., Mrs. C. M. Snow, Dr. W. G. Templeman, Professor F. E. Weiss, F.R.S. and the John Innes Horticultural Institution.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Professor James Eric Smith, Mr. Stanley John Hughes, M.Sc., Mr. Alan Philips Graham, M.A., Mr. Ronald William Keay, M.A., B.Sc. and Miss Eunice Sylvesta Lorraine Jones, M.Sc.

The PRESIDENT reported the deaths of Professor William Eade Agar, Mr. James Inch and Colonel Austin Edward Armitage, Fellows; and Professor Emile Topsent, Foreign Member.

The PRESIDENT announced that the Council had decided to hold a Ballot for the Election of Fellows on 22 November 1951.

Certificates of Recommendation for Election to Fellowship were read for the first time in favour of the following :—Miss Ruth Mary Badcock, M.Sc., Professor Richard Eric Defoe Baker, M.A., Ernest Chambers, Leonard Victor Hand Gingell, S. Z. Hasanain, M.Sc., Ph.D., Vernon Hilton Heywood, B.Sc., John Barns Hunt, George Jackson, B.Sc., Theo Simpson Jones, B.Sc., M. S. Mani, M.A., D.Sc., Clifford Mortlock, D.Sc. and Kasin Suvatabandhu, B.Sc.

A Certificate of Recommendation for Election to Ordinary Associateship was read for the first time in favour of Dennis William Wood, B.Sc.

The PRESIDENT announced that the South London Entomological and Natural History Society had invited members of the Linnean Society to attend their Annual Exhibition to be held in the Rooms of the Royal Society on Saturday, 27 October; and to submit exhibits.

The PRESIDENT announced that the title of the Hooker Lecture to be given on 22 November by Mr. I. H. Burkill would be :—

‘ Habits of Man and the origins of the cultivated plants of the Old World.’

The following communications were read and discussed :—

Mr. R. A. BLAKELOCK. A possible new species of the British Flora *Diapensia lapponica*. (Exhibit.) (Discussed by Dr. George Taylor.)

Mr. F. KINGDON-WARD. The Lohit Valley in 1950. (Discussed by the President, Mr. I. H. Burkill, Dr. E. D. Merrill, Dr. W. B. Turrill, Dr. E. J. H. Corner, Colonel F. C. Stern, O.B.E., M.C., Dr. George Taylor, Dr. W. B. Gourlay and Mr. F. C. Grigg ; Mr. Kingdon-Ward replied.)

THE LOHIT VALLEY IN 1950

By F. KINGDON-WARD.

The Lohit (or Lohit) is one of that fascis of rivers, familiar to students of South-east Asia, which for several hundred miles flow parallel to one another and at no great distance apart, confined by high narrow ranges of mountains each to its own deep gorge. The others are from west to east, the Taron (or Irrawaddy), Salween, Mekong and Yangtze. Even the Tsangpo (or Dihang) may belong to the same epoch.

The belt of country traversed by these rivers (which is some 500 miles wide) is elevated and must be regarded as a southern extension of the Tibetan plateau ; its western flank, fully exposed to the monsoon blowing over Assam, has been deeply eroded.

The main Tibet plateau was elevated in a series of east-west folds, and it seems surprising that this extension of it should show a north-south alignment. However it is clear from the evidence of plant distribution that this too originally formed part of a great east-west uplift, and that the north-south grain is a secondary phase brought about by these rivers cutting parallel gorges through it.

The Lohit river flows down the eastern edge of this high land which extends as far south as the Tropic of Cancer ; but unlike the other rivers named, the Lohit gets no further than the 28th parallel, then turns away abruptly to the west, to reach the nearest plains ; it is in fact the most eastern tributary of the Brahmaputra.

Though nearly 300 miles in length the Lohit is nowhere navigable. Even on its 50-mile journey across the Assam plain, so suddenly does it debouch from the hills and spread out, that it immediately drops huge quantities of sand which the current can no longer sustain, thus blocking its own channel. Hence the Lohit is a comparatively useless river, though it would probably serve to float timber in small quantities.

The whole course of the Lohit is sharply divisible into two contrasted parts : (i) a western flowing limb which occupies a water worn valley, showing no clear evidence of ever having been glaciated ; and (ii) a southern flowing limb which occupies a gorge cut in a heavily glaciated valley.

In the early spring of 1950 my wife and I travelled up the Lohit valley, from Sadiya on the north bank (about 20 miles above the confluence of the Lohit with the Brahmaputra). The road goes east through sub-tropical Indo-Malaysian forest to the foot of the hills 40 miles distant. This section was covered by truck in three hours. At Denning (48 miles) we left the Lohit

(and the truck), from this outpost (2,400 feet) a bridle path crosses the first range of hills by the Tidding Saddle (6,000 feet) and, descending to the Tidding river, becomes a mere jungle track. On the third day's march we found ourselves back by the Lohit, now flowing swiftly in a deep narrow valley.

The foot-hills' Indo-Malaysian forest includes a good many deciduous trees, such as *Bauhinia variegata*, *Sterculia villosa*, *Kydia calycina*, *Erythrina*, *Acrocarpus*, *Melia*, *Dalbergia*, *Bombax*, *Albizia* (several species) and others; but it is on the whole overwhelmingly evergreen, partly no doubt because the deciduous species do not all shed their leaves at the same time, the majority going bare in the cold weather, but some in the hot weather, if for a shorter period. That the forest should be mainly evergreen is not surprising.

Nowhere is the annual rainfall less than 90 in. and at the foot of the hills it rises to 200 in., while a fortnight without rain, even in the 'dry' season is unusual, and winter mist keeps the forest moist. In the summer equatorial temperatures are the rule; and frost is unknown. More important is the constant high humidity.

Such deciduous trees as are met with are generally found growing on well-drained sandy and gravelly soils, especially on river banks on the plain, submerged for longer or shorter periods during the rainy season, but exposed to a hot sun during the dry season. In fact these river banks often carry a belt of deciduous forest composed largely of the trees mentioned. Conspicuous also along these low river banks are dense thickets of *Calamus*; while in the forest occur groves of the reed-like red-fruited palm, *Pinanga gracilis*. The bulk of the plains and foot-hills forest is however, evergreen, abundant species being *Terminalia myriocarpa*, *Duabanga sonneratioides*, *Talauma hodgsoni*, *Styrax*, *Glycosmis*, *Castanopsis indica* and many Lauraceae, Euphorbiaceae, Araliaceae, and a great variety of *Ficus*, including the largest strangling species*. Above 2,500 ft. *Caryota urens* is common, and above 4,000 ft. a very tall *Michelia*. On the other hand, Dipterocarps, so characteristic of the equivalent Burmese jungle 2° further south, are peculiarly rare, nor did I see *Engelhardtia spicata*. After reaching the Lohit again, beyond the Tidding river, the track follows the right bank for twelve or fourteen days' march, never more than a mile distant from it, nor more than 1,500 ft. above it. The forest is at first similar to that of the outer foot-hills, though with fewer deciduous species. I noticed *Cedrela*, *Elaeocarpus*, *Acer*, and other trees; above 4,000 ft. *Prunus cerasoides* (flowering November) is scattered.

Four days' march beyond the Tidding river, a distinct change in the appearance of the valley is apparent; terraces become prominent, up to one or two hundred feet above the Lohit. Now the flanks of the valley are seen to consist of multiple ranges, rising one above the other, this being due no doubt to increasing erosion. These double and triple tiers of hills are especially noticeable blocking the tributary valleys, which follow very tortuous courses. Looking up the main valley, in a south-easterly direction, the mountains gradually increase in height, and in February are presently high enough to be snow-capped. One gets the impression that the Lohit actually rises on the Burma frontier (here the Lohit-Irrawaddy divide) near a group of moderately high peaks to the south-east; and that a conspicuous gash in the hills to the north is occupied by a tributary.

On reaching this gash, however, one realizes that this is an illusion; it is the main stream which flows from the north, turning abruptly through a right-angle while the wide valley to the south-east is occupied by a tributary, thus reversing the outward appearance. Within a short day's march one rounds

* Some of these are deciduous, though bare for less than a month. As however the same species may shed its leaves at any season, I have included them amongst the evergreens.

the Minzong bend, changing direction from east-south-east to almost due north.

Nor is that the only change. Before we reach the corner, we note the appearance of *Ceratostigma griffithii*, a scarlet seeded *Sophora*, and even *Cypripedium villosum*, as significant pointers to a change of flora. Certain hitherto common trees like *Terminalia myriocarpa* and *Castanopsis indica* have disappeared altogether, others, notably *Pinus insularis*, have appeared, at first several hundred feet above the river, but presently on terraces beside the river; by the time we have rounded the bend, this pine is the dominant tree. Its usurpation indicates both a colder climate and a diminishing rainfall. Moreover this is not simply a change of vegetation type, from broad-leaved evergreen forest to Conifer forest; it heralds a break in the flora, a change from one floral region to another, from Indo-Malaysian to something which is a mixture of Eastern Asiatic and Sino-Himalayan. By the time we reach Rima, 35 miles further north, this change is complete; we are now well inside the second division of the Lohit valley already referred to. It is not difficult to recognize what has happened.

Over a long period, while the westward flowing Lohit, which had its source on the Burma frontier, was carving its valley, a glacier occupied the northern gorge. (If at an earlier stage the lower valley also was occupied by a glacier, which is possible, all traces of it have been washed away.) Indeed the whole country north of the Minzong bend was under snow and ice. As the climate grew warmer, the stream from the Rima glacier began to cut a gorge. At first it was a small tributary of the Lohit, but as the glacier retreated it grew steadily larger, until finally it poured more water into the Lohit at Minzong than did the western stream, and itself became the main head water.

Incidentally, just west of the bend, the Lohit cuts across the axis of a high north-and-south ridge which must have supplied (and still does supply) a good deal of water to it. Dapha Bum, an isolated peak 15,020 ft. high stands at the southern end of this ridge, almost overlooking the Sadiya plain.

Three days' march north of the bend the narrow gorge opens out, the spurs cease to overlap, and enormous gravel terraces and alluvial fans appear; the cliffs however continue to be near-vertical for several thousand feet. Here is situated Walong Outpost.

Though from Walong to Rima the dominant tree is *Pinus insularis* with *Quercus glauca* a very hardy oak as second dominant, and bracken undergrowth, the deep gullies sheltered from the strong up-valley wind are filled with broad-leaved mainly deciduous forest in some variety. Here grow *Prunus cornuta* and another *Prunus*, *Ulmus lancifolia*, *Fraxinus griffithii*, *Deutzia*, *Eugenia*, *Philadelphus*, *Ilex corallina*, *Pyracantha angustifolia*, *Elaeagnus latifolia*, *Populus ciliata*, *Cornus macrophylla* and other more temperate trees and shrubs. An unexpected plant here was *Lilium wardii*, which appears to have travelled south of Rima within recent years and is now abundant.

It may be that the pine forest of the dry gorge is no more than a fire preclimax; for the vegetation here has been fired annually for certainly over a hundred years, perhaps much longer. Sometimes these fires get out of hand, and burn for weeks; they are put out only by rain. In March 1950 we saw the cliffs 3,000 ft. above the river well alight and for nearly two months the gorge was filled with smoke from dozens of fires.

But what the climax would be if it were allowed to develop freely is not obvious; no doubt some mixture of pine and xerophytic broad-leaved trees.

The stepped back gravel terraces, with remarkably level surface, and the gently sloping alluvial fans at the mouths of tributaries, now high above the streams, suggest that at one time the whole gorge, at least as far south as Walong, was filled with gravel, sand and boulders to a depth of more than

a thousand feet ; while there is some evidence that it was filled with ice to a height of 6,000 or 8,000 feet above the present river level. No obvious moraines survive, nor perhaps would one expect them to do so, but a mass of boulders and gravel a little above Walong on the left bank, overgrown of course with pine, might possibly be a terminal moraine left by a glacier coming from the east.

Twenty miles north of Walong is Rima, a small but important village situated on the left bank at an altitude of 5,000 ft. Rima owes its importance to its geographical position close to the point where the Lohit river splits into two almost equal branches, one flowing from the north-west, the other from the north-east ; and to the fact that it is the centre of a small district where wet rice can be grown. It is situated at the bottom of a basin, some five miles long by two miles wide, clearly once a lake. Three terrace levels can be seen here, the highest nearly a thousand feet above the river, the lowest about a hundred.

Trees and shrubs found in the valley bottom at Rima include many Chinese and Himalayan species. Here grew *Cotoneaster conspicua* (or a closely allied species), *Berberis*, *Michelia lanuginosa*, *Shoeplia jasminodora*, *Pyracantha angustifolia*, *Pittosporum floribundum*, *Liquidambar*, *Myricaria*, *Mahonia*, *Rosa longicuspis*, *Cudrania*, *Coriaria*, *Ligustrum confusum*, *Leptodermis*, and others.

It is interesting to note that the abundant and brightly coloured berries of *Cotoneaster* and *Pyracantha* last well into April, after which they disappear rather rapidly as the numerous migrant birds come up the valley. It would seem that the comparatively few winter residents do not touch them.

Immediately above Rima, from 7,000 ft., mixed forest, dominated by Conifers, begins. The common Conifers are *Tsuga (brunoniana?)*, *Picea morindoides* and *Pinus armandi*. A little higher up *Abies (webbiana?)* appears and at 9,000 ft. it already dominates the forest, with occasional fine specimens of *Larix*.

The broad-leaved trees of this cool temperate forest are in much greater variety, but are also much smaller, both in girth and height ; consequently they hardly appear from the outside ; looking at the hillsides from a little distance, they seem to be covered with pure Conifer forest, except when the *Michelias (M. doltsopa)* are in bloom ; these *do* show up.

Broad-leaved woody plants include a majority of evergreen species, especially *Rhododendron (R. sino-grande, R. sidereum, R. niphargum* and others), *Ilex pernyi*, *Quercus*, *Isotrema griffithii*, *Skimmia laureola*, *Vaccinium glaucum*, but also many deciduous species as *Cornus chinensis*, *Rosa moyesii*, *Corylus ferox*, *Euonymus frigidus*, *Cotoneaster monbeigii*, *Rhododendron rubrolineatum*, *Sorbus*, *Salix*, *Ribes*, *Lonicera*, *Viburnum* (several species of all these), *Acer campbellii* and *A. stachyophyllum*, *Albizia*, *Enkianthus campanulatus* to mention a few.

The range immediately east of Rima is the Irrawaddy-Lohit divide, culminating in a small group of snow peaks just over 19,000 ft. high. But whereas the Lohit valley is very dry, the Irrawaddy valley 40 miles distant is very wet, filled with mixed forest containing many species not found in the former. The alpine flora is however more uniform, though even here there are outstanding differences on the two sides of the range—as far as exploration has gone.

The ranges west of the Lohit all lie within the drainage area of that river, and of its tributaries, and here occur a number of plants, both temperate and alpine, which have never been found outside this small area : e.g. *Leycesteria crocothyrsos*, *Gaultheria codonantha* and *G. wardii*, *Rhododendron lanigerum* and *R. concinnoides*, *Nomocharis synaptica*, *Primula calthifolia* and a dwarf red 'Sikkimensis' ; and also a number of Himalayan alpine which have

not hitherto been found so far east as China but which nevertheless represent a considerable eastward extension: e.g. *Rhododendron lanatum*, *R. griffithianum*, *Bryocarpum himalaicum*.

The first movements of the flora in South-east Asia in late Tertiary or early Quaternary times must have been east-west following the great earth folds. But there appears to have been no driving force behind it; plants moved much as they do along a railway embankment. They had plenty of time to spread.

Before and during the Pleistocene glaciation a more rapid north-south movement set in under the influence of a powerful driving force, namely the creeping barrage of cold.

By the time the glaciers had retreated, there were two routes by which plants could move northwards into the vacuum left by the ice: via the mountain ranges, and via the newly created river gorges. It was now much more difficult for plants to move east and west by reason of the discontinuity these breaches had made in the folds.

This 500-mile belt of mountain and gorge is the very hub of the movements which the floras have undergone, and the separating is far from complete. Thus we find a strange assortment of plants here—Japanese and Chinese (East Asiatic), Indo-Malaysian, northern and Sino-Himalayan. But until the flora is better known it is impossible to tell the whole story.

The uniformity of the Sino-Himalayan (alpine) flora throughout the 30° or 40° of longitude across which it extends might be expected, since the plateau flora, before the post-glacial blocking-out of the north-south ranges by erosion, would originally have been uniform. It is not surprising that this alpine flora has persisted on the several ranges (the remnants of the plateau), with modifications following a gradual ascent of species as the climate improved.

But the warm temperate flora of the valleys represents no such remnant of a local uniform flora, since the region was never all valley as it was once all plateau; nor did any deep valleys exist until long after the ice had disappeared. This temperate flora must have flowed in from the south. We should therefore expect a larger degree of endemism here than on the alpine ranges, and less uniformity between the several valleys.

However, below about 8,000 feet a surprising number of woody plant species extend both east and west of Rima, from the eastern Himalaya to South-west China and beyond, skipping the high intervening ranges and reappearing in the next valley. I may mention such species as *Corylus ferox*, *Leycesteria formosa*, *Euonymus frigidus*, *Schoepfia jasminodora*, *Viburnum cylindricum*, *V. atrocyaneum*, *Cornus macrophylla*, *C. capitata*, *Ulmus bergmanniana*, *Lonicera henryi*, *Pittosporum floribundum* and *Quercus glauca*, all found at Rima.

A certain number of Chinese species (*Cornus chinensis*, *Alangium chinense*, *Rhododendron oleifolium*) seem to find their western, and a few eastern Himalayan species (e.g. *Prunus cornuta*) their eastern limit here.

This southern prolongation of the Tibet plateau southwards between the gulf of Assam and the Red Basin of Szechwan (both silted up) is centrally placed as regards South-east Asia; and since a number of Rima species extend right across from the western Himalaya to the Pacific coast, it may itself be a distribution centre whence species have radiated.

A complete distribution analysis of the species collected hereabouts, on both flanks of the Lohit-Irrawaddy divide and subsidiary ranges might throw further light on these problems. But it seems doubtful whether it would lead one much beyond the few broad generalizations which, in the present state of our knowledge of the flora and geological history of South-east Asia, we are already justified in making.

On the night of 15 August 1950 came the great earthquake whose epicentre

was in the Rima district, a few miles from where we were camped. Owing to echoes in the deep gorge, and to the thousands of tons of rock which poured down every mountain scupper, and not less to the sounds of rending and shearing which came from underground, the noise was almost deafening.

From the point of view of the botanist, very considerable changes were initiated, the most obvious of which was the complete sterilization of large areas, from 5,000 ft. to at least 15,000 ft., giving unique opportunity for observations on succession at every level during the next few decades, if competent observers could visit the area.

Because the earthquake took place towards the end of the rainy season, when all snow below the permanent snow line had already melted, the immediate damage in the lower valley and on the Assam plain was less than it was likely to be in the following year, and for some years to come. Stabilization in so steep a country is bound to be slow. Vast quantities of rock were loosened, and big torrents, even the Lohit itself, are likely to be dammed periodically. Moreover the beds of the Lohit and of the Brahmaputra on the plain of Assam are still being raised. The course of the Lohit within its gorge cannot change appreciably; on the plain it can.

An immense amount of timber was destroyed; this was mostly *Pinus insularis* in the Lohit gorge, but some forty species of trees were picked up in the bed of the Brahmaputra in the cold weather of 1950.

One curious effect of the earthquake at Rima was the killing of shrubs on the river banks, which outwardly appeared unharmed. I can only ascribe this to the breaking of the finer roots in the rotting gravel by the tremendous vibration.

Still other consequences followed from the pall of dust which hung over the valley for weeks, and was continually reinforced by rock slides. I found the vegetation everywhere caked with dust, which lay thick on the leaves. Some of this, though by no means all, was subsequently washed into the soil by rain; and this heavy dust film might well cause further loss of plant life.

Great numbers of seeds, and also entire plants, would be carried to lower levels by both flood and rock slip. In this connection it is interesting to note that a *Myricaria* (*M. elegans*) found growing in thickets at Rima appeared on the south bank of the Lohit, opposite Sadiya some years ago, and is well established (or was before the recent earthquake) on the plain, under very different conditions.

Some of the mountain torrents (e.g. the Sap Chu near Rima and the Yepak near Walong) ceased to flow for 24 hours or more. When the dammed up water was loosed, it scoured out the forest, brought down thousands of boulders, and plastered several feet of dark stinking sand on the rocks.

All these incidents affected the vegetation in greater or lesser degree, directly or indirectly.

The rocks at Rima consist mainly of fine-grained biotite granite and of biotite-hornblende gneiss, with a great deal of felspar, so that the stepped mountain sides everywhere show white as driven snow. In the lower valley, near the debouchment of the river on to the plains, the underlying rocks consist largely of soapstone and chloritic schist. It is worth noting that the evergreen broad-leaved rain forest of the outer hills was no more effective in holding the mountains together than was the burnt pine forest.

There are two hot springs in the neighbourhood, one in the river bed a mile or two above Walong, at about 4,000 ft. altitude, and one half way up to the Diphu La, a few miles below Rima, at about 10,000 ft. While severe earthquakes are comparatively common in Assam, we have not in the past heard much detailed news of those, however violent, which take place in such dynamic and sparsely populated regions as the Lohit valley; nor are we more likely to do so in the future.

It is quite conceivable however that many features of this region difficult to account for by any slow geological process of wear and tear, do in fact owe their origin to such violent movements. (At Rima, throughout the main shock, the crustal movements were, or appeared to be, *vertical*, not *horizontal*, and of great rapidity.) If the slow action of fitness survival is not by itself enough to account for the evolution of species (and few naturalists today believe it is) and more violent jumps are considered not merely possible, but inevitable, it seems equally probable that the form of the land surfaces may also owe something to the more violent processes of nature which are seen—and felt.

We are left wondering whether there may not be some connection between the two sets of phenomena; whether in fact such convulsions as that of 15 August 1950 may not affect the germ plasma of some plants to such a degree that they produce monstrosities, that is, aberrations from the normal. It may be that plants too can suffer from shock.

In this connection it is worth recalling that, little as the region has been explored, a number of remarkable plants have been discovered there. In 1949, for example, we found just south of the Lohit valley an extraordinary *Euonymus* with enormous fruits and an even more extraordinary *Camellia*, also with enormous fruits. *Leycesteria crocothyrsos*, and other endemic species have already been referred to. However, only the future can tell whether this great earthquake directly influenced the vegetation; its last effects have not been seen yet.

We stayed in our camp at Rima 23 days following the earthquake, unable to travel up or down the gorge on the left bank, and unable to cross the river. When finally a new rope bridge was fixed in position, the 20 miles to Walong, across the shattered cliffs, took us four days.

The only way out of the Lohit was the way we had come in; but we were held up in Walong five weeks before we could make a start, and the hazardous march to the plains took another 20 days. We had plenty of time to observe the frightful destruction wrought; and a difficult ascent of the broken mountains above Walong to over 10,000 ft. showed how extensive was the havoc on the eastern range to the very summit.

We reached Sadiya on 6 November, twelve weeks after the earthquakes, having come on foot all but the last 30 miles across the plain. Indeed, if walking was the only way to reach Walong, much more was it the only possible way to get from it.

PROCEEDINGS OF THE GENERAL MEETING ON 25 October 1951

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 11 October 1951, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Professor L. R. Parodi, F.M.L.S., Mr. H. G. Suggate, Professor F. E. Weiss, F.R.S., and the International Union for the Protection of Nature.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows:—Miss Lilian Haywood Eaton, B.Sc., and Mr. Peter Bernard Platts.

The PRESIDENT reported the death of Dr. Stephen King Montgomery, Fellow of the Society.

Certificates of Recommendation for Election to Fellowship of the Candidates named in the Minutes of the General Meeting, 11 October 1951, were taken as having been read for the second time.

Certificates of Recommendation for Election to Ordinary Associateship were read for the first time in favour of Alan John Brook, B.Sc., Ph.D., and Fred Ronald Jones, B.Sc.

The following communication was read and discussed :—

Professor S. ZUCKERMAN, C.B., F.R.S. Some features of the Anthropoid Skull of Apes. (Discussed by Mr. R. J. G. Savage, Dr. W. Warwick James, O.B.E., Professor A. J. E. Cave and Dr. A. Tindell Hopwood ; Professor Zuckerman replied.)

SOME FEATURES OF THE ANTHROPOID SKULL OF APES

By S. ZUCKERMAN.

Department of Anatomy, University of Birmingham.

Abstract, —

A number of features of the adult anthropoid skull can be related to the eruption of the permanent teeth. Among them is the sagittal crest.

The relative extent to which the anthropoid muzzle grows is related to the size of the permanent teeth, and in so far as these are more prominent in the gorilla than in, say, the chimpanzee, the muzzle of the gorilla seems to be relatively more prognathous than that of the chimpanzee. Furthermore, as the whole skull increases in weight, due to the development of the cranium and more particularly of the muzzle, it becomes remoulded as a result of the extension of the muscles of mastication, and of those which support the skull on the vertebral column. Consequently its 'balance' also alters.

Thus, as the jaws increase in size, the temporal muscles grow upwards over the cranial vault, and also backwards to meet the upwardly-extending nuchal musculature. In a small proportion of male chimpanzees and female gorillas, and in most male gorillas, the two temporal muscles meet in the mid-line above, and as a result of their further growth, a central keel of bone—the sagittal crest—develops. Before this happens, the upwardly-extending nuchal muscles, including the trapezius and sterno-cleido-mastoid muscles, meet the backwardly-extending temporal muscles to form an occipital or nuchal crest. As this change takes place, the disposition of the nuchal area of the skull alters. Simultaneously the development of the sternomastoid, the splenius capitis, and longissimus capitis muscles becomes reflected in changes in the mastoid region. During the whole of this process, the occipital condyles appear to 'migrate' backwards, and changes occur in the inclination of the foramen magnum. The migration is only relative, since the general position of the foramen on the vertebral column cannot alter with the growth of the skull and body.

The position of the occipital condyles relative to the base of the cranium provides a measure of the balance of the whole skull on the vertebral column, and of the relative growth of the pre- and post-condylar parts of the skull.

Investigation shows (Ashton & Zuckerman, 1951) that the index expressing the ratio of these two segments (the condylar-position index) in the australopithecine skull, *Plesianthropus* 5, is very much closer to the range found in subhuman Primates than to that of existing or extinct types of man. The far closer approximation of the relative 'position' of the condyles in *Plesianthropus* to that in the apes, as opposed to man, either living or extinct, is also apparent when a comparison is made with ape skulls in which the inion is not prolonged backwards as in adult skulls (Ashton & Zuckerman, 1952). If the australopithecines, as represented by *Plesianthropus*, did stand upright, the only conclusion one can draw from the condylar position index is that the head was balanced as in apes rather than as in man.

This inference is strongly supported by the fact that the most recent australopithecine finds (*Paranthropus crassidens*) are of skulls which possess sagittal crests. Unfortunately, the occipital part of the skull was deficient in the two specimens in question (both assumed females). In all respects the crests appear to be similar to those which occur in great apes, and quite unlike the kind of 'crest' which occurs in *Pithecanthropus*, Rhodesian Man, and occasionally modern man. The sagittal crest is also associated in the fossils with a powerful supraorbital torus. Unless *Paranthropus crassidens* is the one exception to a morphogenetic process common to all known primates, its possession of a high sagittal crest presupposes the presence of a powerful and shelf-like occipital torus, and of the powerful neck muscles usual in the great apes.

The only circumstances in which such a conclusion would not apply would be if the mechanism of the jaws in the australopithecines were different from that in the great apes. A detailed analysis of the anatomy of the mandible and temporo-mandibular joint shows that there are no fundamental differences in the way the jaws work in man and apes. Moreover, a study of dental attrition shows a remarkable similarity in the order of appearance and coalescence of facets of wear in the teeth of apes and men. The presence of large canines does not preclude the ape from moving its mandible in the lateral plane.

It has been suggested by some workers that the teeth of the australopithecines became worn in human fashion. If they did, they must *ipso facto* have become worn in the same way as do apes' teeth.

The implication of these studies is, therefore, that *Paranthropus* carried its head on the vertebral column far more like a gorilla than a man.

These various points are discussed in greater detail elsewhere (Zuckerman, 1953).

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- ASHTON, E. H. & ZUCKERMAN, S. 1951. Some cranial indices of *Plesianthropus* and other primates. *Amer. J. phys. Anthropol.*, **9**, 283-296.
 —. 1952. Age changes in the position of the occipital condyles in the chimpanzee and gorilla. *Amer. J. phys. Anthropol.*, **10**, 277.
 ZUCKERMAN, S. 1953. Correlation of change in the evolution of higher primates. Chapter in *Evolution as a Process*. (In the press.)

The following papers were read in title :—

- 'Notes on British Hyacotheres.' By G. GAYLORD SIMPSON, F.M.L.S. [*Journ. Zool.*, No. **284**.]
 'A Review of the African species of *Blechnum*.' By E. A. C. L. E. SCHELPE, F.L.S. [*Journ. Bot.*, No. **355**.]
 'The genus *Pandanus* in the Mascarene Islands.' By R. E. VAUGHAN, O.B.E., Ph.D., F.L.S. and P. O. WIEHE, M.Sc., F.L.S. [*Journ. Bot.*, No. **356**.]

- 'Expedition to the Gughé Highlands (Southern Ethiopia) 1948-49; Coleoptera, Carabidae, Pterostichinae.' By S. L. STRANEO. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) [*Journ. Zool.*, No. **285**.]
- 'Expedition to the Gughé Highlands (Southern Ethiopia) 1948-49; Coleoptera, Carabidae.' By P. BASILEWSKY. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) [*Journ. Zool.*, No. **285**.]
- 'Expedition to the Gughé Highlands (Southern Ethiopia) 1948-49; Coleoptera, Dascillidae'. By MAURICE PIC. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) [*Journ. Zool.*, No. **285**.]

**PROCEEDINGS OF THE GENERAL MEETING ON
22 November 1951**

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The PRESIDENT welcomed the presence at the Meeting of Members of the Stockholm Committee for the Nomenclature of Plants in Cultivation and the International Committee for the Nomenclature of Garden Plants.

The Proceedings of the General Meeting held on Thursday, 25 October 1951, having been circulated, were taken as read, and confirmed.

The PRESIDENT announced that HIS MAJESTY THE KING OF SWEDEN, recently elected an Honorary Member of the Society, had signed the illuminated vellum sheet prepared for insertion in the Roll and Charter Book.

A special Vote of Thanks was accorded to Mr. John H. Robins for his gift of the correspondence of Dr. Richard Pulteney, F.R.S., F.L.S. (1730-1801).

The following were thanked for gifts made to the Library since the last Meeting:—Sir Nigel Ball, Bt., Mr. F. W. Gibbs, Mr. Michael Haworth-Booth, Dr. William McCartney, Mr. John H. Robins, Mr. J. G. Skellam and the Royal College of Surgeons of England.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows:—Mr. Reginald Arthur Peachey, Mr. Robert Joseph Gay Savage, Dr. Michael Robin Alexander Chance and Dr. Bertram Maurice Hobby.

The PRESIDENT reported the death of Arnold Swaffer, an Ordinary Associate.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS:—Miss Ruth Mary Badcock, M.Sc., Professor Richard Eric Defoe Baker, M.A., Ernest Chambers, Leonard Victor Hand Gingell, S. Z. Hasanain, M.Sc., Ph.D., Vernon Hilton Heywood, B.Sc., John Barns Hunt, George Jackson, B.Sc., Theo Simpson Jones, B.Sc., Professor M. S. Mani, M.A., D.Sc., Clifford Mortlock, M.Sc. and Kasin Suvatabandhu, B.Sc. ORDINARY ASSOCIATES:—Alan John Brook, B.Sc., Ph.D., Fred Ronald Jones, B.Sc. and Dennis William Wood, B.Sc.

The following communication was read :—

THE HOOKER LECTURE

By Mr. I. H. BURKILL, F.L.S.

HABITS OF MAN AND THE ORIGINS OF THE CULTIVATED PLANTS OF THE OLD WORLD

(With 9 text-figures.)

I have been interested in the means of living that the jungle tribes of the East possess and naturally in the Andamanese as among the lowest. They exist without any cultivation as neolithic relics and have survived because of the barrier that the ocean afforded, adjusting their numbers to their food supplies by means of an antagonism to any who might intrude so fierce as to separate one tribe from another completely and to lead to the existence of several collateral languages within the islands. They hunt and they fish and are food-gatherers of all the vegetable stuff that they find edible. I have collected together the available information on this and find that the whole of it is derived from perennial plants, and that it comprises almost nothing which can be eaten without cooking—most of it not without cooking with wood ashes to make it such that even their inured digestions can digest it. One of their best foods is the tuber of *Dioscorea glabra* Roxb., for which they dig assiduously. Their improvidence is so great that if in past times the land held any tuber requiring less digging, they must have destroyed it by over-exploitation. But today they make *D. glabra* a crop-plant to the small extent that the elders issue a taboo on the digging of the yams in the season of new growth, saying that the rain-god, Puluga, needs the yams at that season; and they issue a like taboo to protect the seed-crop of *Entada scandens* Benth. and the palm-cabbages of *Caryota* (see E. H. Man, *The Andaman islanders*, p. 85 of ed. 2, 1932).

Cousins of the Andamanese are the Semang of the northern forests of the Malay Peninsula. They are in a slightly worse position because they do not have access to the sea; but R. J. Wilkinson suggested that they had the resources of the shore until recent times (Papers on Malay subjects: 'Peninsular Malays', p. 1, 1920). They wander in family groups in the densest and most beast-infested forests, feeding on the tubers of wild yams and aroids, etc., and move forward at very short intervals as they exhaust the available food supplies. As with the Andamanese, their vegetable food is derived entirely from perennials. Now and then the fruiting of a wild durian tree or an unusual abundance of wild fruit induces a halt of longer duration in which they clear the ground under the fruiting trees the better to get the falling fruit; but this is not tilling. If they venture to push a few sugar-canes into the soil, the wild elephants destroy them before their return. Father Schebesta, who described these simple folk in his *Bei den Urwaldzwerger von Malaya* (1927), sent me specimens of the wild *Dioscoreas* that they eat and I gather that it is every one available.

The Andamanese and the Semang are negritos. There is no future for such; and their past has been millennial stagnation. The forest masters them; and in it they are in very truth agents with the wild pigs in the natural selection of the wild yams, maintaining to their own disadvantage the deep-rooting habits by destroying any variation towards surface-rooting and any diminution of protective nauseousness.

I would here point out that wild yams are basic among food plants of humid tropical forests; and that wherever such forests occur the genus *Dioscorea* is at home—a food in a raw state for such animals as can root for the yams,

and a food after cooking, sometimes rather prolonged cooking and even tedious preparation, for Man, yet attractive enough for a score of species to have been taken into cultivation, some here, some there ; but the Andamanese have been too witless. Yet I must put forward an excuse : *Dioscorea glabra* propagates itself by seed, which seed is certainly formed freely ; but if it be sown, several years pass before there are tubers large enough for use ; and it would indeed be asking much to ask one who has never tilled to conceive the idea that by tilling a harvest so remote could be of benefit. To the verdict—too witless, extenuating circumstances may be admitted.

Perennials are intractable collectively. Tillage did not begin with them but when intelligent men contacted annuals favourably prepared by Nature. This happened in several parts of the world, but undoubtedly earliest in south-western Asia, where likewise was the first domestication of animals, the first urbanization, the invention of the wheel and the first use of iron weapons.

It is generally agreed that Man, being at the time a food-gatherer, with hunting his most enterprising form of food-gathering, domesticated the Dog as a companion in the hunt. After that there was a wandering into the New World which took the Dog, but not habits of tilling. In the Old World Man proceeded to domesticate some of the animals that he hunted. They would be of similar size to his companion, the Dog, and assuredly Sheep or Goats. Unfortunately the history of this event is difficult to piece together : but this fact is sure—that sheep never lived in forests but in open country where they sought security by agility on broken hillsides, and by that habit they thrived upon the mountains ; but Man put an efficient protectiveness between them and any desire for mountains and certainly grazed his flocks over hills and wide plains alike through the quarter of Asia mentioned. Tillage dawned among these herdsmen of sheep at that time of the year when abundant spring pasture enabled them to dally and, dallying, to try to increase the supply of vegetation. The opportunity was created by Nature ; she makes grass prairies where the summer rain is inadequate to maintain trees and creates conditions that favour annuals. It happened—I think no other verb than happen is appropriate—that Nature put in the way of these herdsmen annual grasses whose provision for survival lay (i) in the abundance of their output of seed, and (ii) which grew gregariously, so that when the seed was ripe and was plentiful it could be collectively harvested, and (iii) was edible. Moreover, the foliage before harvest time was good food for the sheep ; and the seed after harvest was in an ideal condition for storage. It was impossible for Man to overlook the advantage of increasing the supplies of a grass so eminently desirable which, even if he were forced to move to other pasture too early for harvest, could be given over to the sheep. The double lien drew grasses into what I believe was the earliest sustained tillage in the world. The cultivation would be slovenly in the extreme, as some is always. Gaedukevich (quoted from the *S.-W. Journ. Anthropol.*, 6, p. 21, 1950) describes Kirghiz of the Ust-Urt who, on finding a patch of bared silt, broadcast grain over it and then drive the sheep forward to trample it in. The harvest would be by plucking the individual spikes if large enough, or there might be found other ways ; Pliny described the use of a comb for millet as customary in Gaul, and a famine-stricken native of India will harvest grass seed by sweeping with a winnowing basket or strip of cloth. Such ways of getting in the return would be readily found. The habit of protecting the growing crop had to be acquired. That the tiller should be able to dally meant that he had to possess enough food on the hoof to be able to await his harvest. The all-compelling difference between him and the Andamanese lay in that he was a capitalist and secured.

It may be well to point out that there is a difference between a cultivated plant and a cultigen, that a cultigen carries in a heritable condition some character, qualitative or quantitative as we assess it, derived from cultivation,

and that there is only one time in the life of a plant when a character can be impressed, namely the time when Man determines on his re-sowing. Therefore it matters greatly how often this time comes round—yearly or at wider intervals ; and for two reasons, one, merely the arithmetic fact that in ten years an annual offers ten opportunities, but a perennial perhaps not more than one, or even fewer ; the other and overpowering reason, that Man, particularly early Man, might keep on one course if he had to repeat his sowing year by year, but was sure of losing direction when the occasions were more spaced. In fact Man drifted into establishing characters for his cultigens. What he did was to make a gift of free earth to a wild plant in the hope of a return ; and with a good return he was induced to repeat ; but on repetition the seed might come again from a wild source, so that he did no more than repeat the first experiment. It was only when he needed to keep seed from one generation to another that a cultigen could be originated. That would come with attempts to extend the range beyond the plants natural limits, in which, really by accident, the essential isolation would be introduced. Acclimatization, the first property of a cultigen, would be induced according to the difference between the new and the natural habitat. It is always to be remembered in seeking for origins of cultigens how their chances of fixation are increased away from home.

A thought comes to mind here—a wild plant to be worth tillage straight from the wild stage had to be rather outstanding, or of a group of a few that were outstanding. Man must have worked on a narrow front.

As Man acclimatizes he selects unconsciously for simultaneous seed-bearing, for he tends not to harvest seed produced abnormally early and loses seed produced abnormally late. At the same time he unconsciously selects against shattering or scattering, for he loses the seed of plants which do this. By protecting his crop against birds which are deterred from feeding by awns, he diminishes the value of these, making awned and awnless plants equal contributors to his seed for re-sowing ; and the loose panicle, difficult for the perching of a bird, ceases to be an asset necessary for success. In so far as the inducing of such characters was subconscious, they are marks of antiquity ; and the character of area goes with age because acclimatization was subconsciously operated.

The system of tillage now in mind began, as postulated, with cereals. Hehn, who became a great authority on the spreading of its plants into Europe, commented (*Kulturpflanzen u. Haustiere*, p. 210 of ed. 7, 1902) that when Man had established the habit of cultivating cereals, he would quickly pass on to cultivating pulses. I agree. Meanwhile Man remained a food-gatherer of supplementary food, notably greens, which, when they were weeds that volunteered in his tilled land, would be culled thence as well as from the untilled land, until they became more easy to obtain from out of the crops than from elsewhere, whereafter they would be given a place of their own. Much play has been made lately of 'crops from weeds' ; but every crop plant after the first was a weed once. The interest is not therein but in discovering when they passed from weeds to crops. Of competition in the soil we know almost nothing (see Russell's *Soil conditions and plant growth*, ed. 8, p. 492, 1950) ; but the experiments in competition of Barley with weeds commenced by Dr. H. H. Mann and T. W. Barnes are a beginning (*Ann. appl. Biol.*, **32**, 15, 1935 ; and **34**, 252, 1947).

Plants accepted for cropping as greens would be such as matured among the cereals and pulses, and all the oldest would be short-lived. After the adoption of (i) cereals, (ii) pulses and (iii) short-lived greens, it is by no means unreasonable to think that Man would grow (iv) oil-seeds such as the genus *Brassica* furnishes. But when he found it possible to live on the produce of one locality in a static way he would proceed to (v) what an agriculturist understands as 'roots' ; then (vi) herbaceous fruits, (vii) fibre and dye plants and long afterwards (viii) woody plants, chiefly fruit trees and (ix) various

industrial plants. A large measure of urban development had to occur before the entry of group ix.

Immediately after the War of 1914-18 the Soviet Republics organized a great hunt for material for their domestic agriculture and put it under the direction of Professor N. I. Vavilov. Vavilov wrote of it that it consisted of "numerous expeditions sent to different parts of the globe" and that they "collected an enormous amount of material". The seeds brought home were sown in experimental stations through Russia and a vast herbarium built up for record and reference. There has never been and possibly may never be another effort of its kind on so large a scale. Its size was against immediate fruition and some of the earlier published results bear the marks of preconceptions that invite criticism. Vavilov, who had travelled to gather material in Europe, Afghanistan, China, Abyssinia, North and South America, attended a Congress in London in 1931 of the History of Science and Technology and read a paper

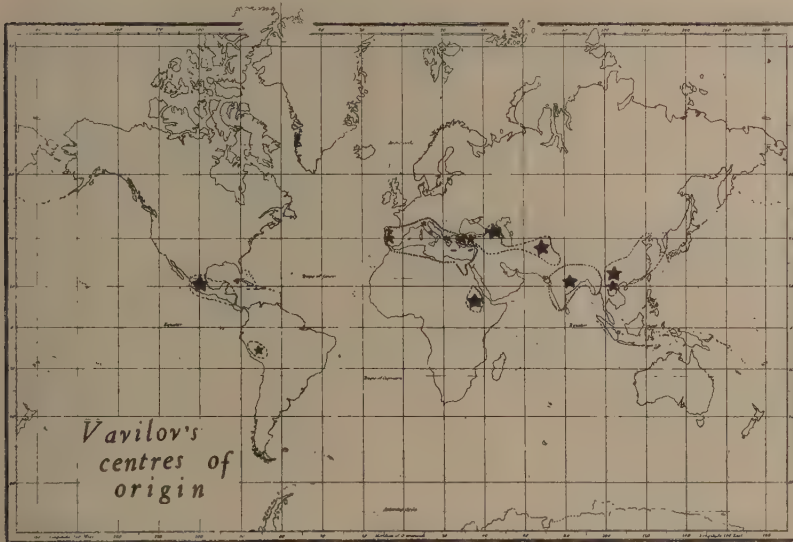


FIG. 1.—The seven centres which Vavilov named as sources of the whole world agriculture. The larger the star the more important the centre.

entitled "The problems of the origin of the world's agriculture", wherein he stated that "there are seven fundamental independent world centres of origin of cultivated plants . . . chiefly confined to the tropical and subtropical mountain regions" and that these "have given rise to the whole world agriculture". That the reader may know what centres he postulated, I have made fig. 1 from his map. Five of the centres are in the Old World and two in the New. He calls the five centres, Mediterranean, South-western Asia, India (excluding from it the north-western part), Eastern and central mountainous China and mountainous East Africa, chiefly Abyssinia. Four years after the Congress he varied his plan a little, dividing South-western Asia into Near East and Central Asia, and cutting off from India a centre which he called the Indo-Malayan centre. His procedure for determining centres was to take a map, and to select the cultigens of importance, then to mark on the map where the recognizable races of these cultigens are found: where the marks lie thickest there is a centre. The method he calls the differential method. It has the

fault of taking the whole of its evidence from the plants and disregarding the cultivator. The further claim that the centres are all in mountains embodies the fault. Every phytogeographer is aware that mountains are rich in species, richer than plains. This is explicable by the crowding of microclimates into mountains whereby the chances of survival of variants are multiplied. Useful and useless plants are subjected to the same opportunities; as they vary, so may their varieties be able to persist, but those of the useful plant do not become cultigens until man isolates them. And the persisting variability of cultivated plants in mountains is chiefly a consequence of incompetence in agriculture of the average mountaineer. Mountain chains are therefore a good field for the skilful plant-breeder to explore for new forms, but not a sure source for the world's cultigens.



FIG. 2.—Dispersal of the genus *Olea* in the world. *O. europaea* in black on the left; the rest of the genus within the black lines.

The value of isolation is all-compelling. Natural geographic isolations have led to some of Man's greatest successes—cases in which Nature made the opening and Man succeeded. I illustrate this by a map of the distribution of the genus *Olea* with the area of the Olive (*Olea europaea*) in black. Man brought the Olive forward in natural isolation, for as the map shows, its area is outside that of the rest of the genus. The Date (*Phoenix dactylifera*) is extra-marginal to the inferior species of its genus. The Fig (*Ficus carica*) is marginal within its great genus. The Mango (*Mangifera indica*) has but one associated species of its genus in that part of India where it originated, inferior species being concentrated in Malaysia. The Coconut palm (*Cocos nucifera*) developed far away from the rest of the genus *Cocos*. The importance of isolation

cannot be exaggerated: Man had not spent millennia in effecting so little ennoblement, if the isolation accompanying his effort had been more. Man, as I see the problem, was more likely to succeed in making a cultigen on the margin of a mountainous area than within it: and the differential index is a pointer for the search of material for ennoblement: the actual ennoblement was likely to be marginal.

I find it instructive to take the countries which Vavilov names as holding his 'centres' and to make from them the map of fig. 3. I have numbered the compartments so constructed from west to east, and their boundaries are



FIG. 3.—Compartments of origination, being the political units named by Vavilov as holding his centres.

political boundaries. It is axiomatic that if the political boundaries be firm, they represent cultural discontinuities, past or present, such as cannot but be barriers to the dispersal of cultigens. As fig. 3 shows, the compartments make a belt across the map, the southern boundary of which is either sea or desert. A few words on the recognition of the desert as a boundary are called for because there has been speculation on the degree in which a milder climate in the Sahara during the millennia following the passing away of the Glacial Epoch would let economic plants migrate. Most particularly this speculation has turned on the value of the Nile valley as a highway for migration. Growth in the severity of the desert must be admitted; and the problem becomes the ascertaining of conditions at a date when cultivated plants existed. Surely we may push out of the argument any period before 8000 B.C. and almost as confidently any period before 7000 B.C. But of a certainty at 4000 B.C. the Nile valley margin in Middle Egypt was not quite desert; hunters sought food on it, and that proves the presence of animals; and villagers made receptacles of

ostrich eggs, which proves the presence of ostriches. But I can find no reason for thinking that cultivated plants passed from the Mediterranean margin to Guinea or from Guinea to the Mediterranean margin at any remote period. It may be pointed out that the northern Sorghums were originated by tillers debarred from the Mediterranean by wide-waterless country, who concentrated on them in the absence of cereals from beyond the sands. The Nile valley offers a more delicate problem; and the theory of some Egyptologists that the great reverence which Egypt showed for the land of Punt, i.e. the tropical south, rose from the rulers of historical Egypt having come thence, has been used in arguing that there was early contact. But Egypt's way thither was by sea: it left the Nile valley near Thebes for the harbour of Kosseir, abreast of Thebes, and continued by coasting (see fig. 6 on p. 32): and great empty spaces by land separated Thebes from the mountains of Erytrea and Abyssinia. Petrie (*Hist. Egypt*, 1, 12, 1894) points to Kosseir as being on the way by which the ruling race would come; and if so, caution is certainly necessary in postulating pre-historic connections up and down river. I shall later need to show that the way out of Africa for certain economic plants was across the southern end of the Red Sea to Arabia and not to Egypt.

I return to fig. 3. The northern boundary of the belt is weaker than the southern, by reason of gaps between the great mountains over which it passes. One gap, the wide gap between the Caucasus and the Himalaya, is partly blocked by deserts; that between the Alps and the Black Sea has been very penetrable, so that plants from the Near East could reach the uniform, fertile, easily tilled soils of the Danubian plains.

Of the north-to-south partitions, Vavilov lays down that between compartments 1 and 2 on the wrong side of Egypt. Gibbon's words "accessible only on the side of Asia whose revolutions in almost every period of history Egypt has humbly followed" can be applied to Egypt's crops, and Egypt must be assigned to the Near East instead of the Mediterranean. By a transfer of the partition there is left a more natural Mediterranean compartment. Vavilov's revision of 1936, whereby he recognized that the south-western Asiatic centre is appropriately divided into Near East and Central Asia or as I shall call it Inner Asia, is convenient. The two halves manifestly grew apart as Man became less nomadic. In an interesting contrast the components of the Mediterranean grew together as Man got control of the sea. Vavilov uses the Thar or Indian desert to delimit his Inner Asia towards India; it serves. His centres further east are unnatural and I have prepared a map (fig. 4) to correct this. About 3000 B.C. there was a civilization in north-western India, the 'Indus civilization', into which excavations at Mohenjo Daro and Harappa have given an insight. It was in touch with contemporary civilization at the head of the Persian Gulf. At the same period, according to the Chinese historians, nascent China was ruled by a king (2737-2705 B.C.) named Shen-nung—the name means divine labourer—who invented agricultural implements and taught tillage. The date is unreasonably late for a beginning of tillage in their part of the world, but could be a date for the introduction of metal tools, as copper and bronze were in contemporary use in the Indus civilization. The Chinese were able to keep their line of agriculture; but the Indus civilization went down. On its ruins came the Aryans. Carleton has written (*Buried Empires*, p. 163, 1939) how greatly it would clarify history could we discover that Mohenjo Daro was destroyed by the Aryans; but all we know or surmise is that about 2000 B.C. and continuing later over a long time, pastoralists bringing their establishments with them wandered from the north-west into the Indus area and when they were numerous enough, being well led, say about 1500 B.C., they took possession of the land. It is surmised that they were led by a sort of knighthood, as were the Kassites, who took Babylon a little earlier. There is no indication that they brought new crops

to India, but that they took over what was already there as they settled. At 1000 B.C. they were centred where the letter 'A' of their name is on the map; then they overflowed round the north of the Thar into the Gangetic plains, perhaps having been strengthened, and if so by a more defined invasion than their original coming. They were now where the letter 'Y' of their name is. By 250 B.C. their expansion had been so great that the emperor Asoka could set up marks of his rule almost anywhere in India. I must define 'India': I use the word for the whole triangle from the Cupuliferous boundary line (see the map) to Ceylon; so delimited, it is very well characterized both phytogeographically and ethnically. No species of the Cupuliferae nor of the Coniferae passes from the north and north-east into the triangle, nor does Mongolian blood, except by infiltration at the Bengal angle. Contemporary



FIG. 4.—A readjustment of the compartments from India eastwards showing by arrows how the migrations of Semi-mongoloids separated the Aryans and the Chinese.

with the Aryan expansion there was expansion of the original China—"a very gradual and massive expansion" (Lattimore) that swallowed up everything in front of it taking possession of new plants and fitting them into a very sound form of agriculture. By the time of Asoka the Chinese advance was approaching the present limits of political China and was shortly to break up the Shan kingdom of Yun-nan: but that was not to close the gap between the Chinese and India, through which migrants came southwards at various times more or less as the arrows on the map indicate, and their invasions put buffers between the Aryans and Chinese which held their agricultural systems apart. The compartments that I recognize have accordingly been regrouped. India is the triangle that I have defined; 'China' will be used for the area occupied by Chinese; 'Indo-china' for the land south of China and east of India;

Malaysia and Polynesia complete the number of the compartments. A contrast of phytogeographic importance between India and China lies in that India receives its rain after its greatest heat ; China receives its rain with its greatest heat.

It has not escaped comment that the Mexican-Central American centre (see fig. 1) is on the same latitude as the belt across Asia ; and the circumstance has been explained by suggesting that the latitude favoured the energy of Man. The explanation is inadequate ; forethought, rather than energy, was the outcome of the latitude. Fig. 3 shows that the latitude varies considerably ; compartments nos. 1, 2 and 3 run together ; and the others are scattered. This suggests that nos. 1, 2 and 3 possess something in common which the others do not possess. I explain the differences in this way ; Man's greatest agricultural development began in nos. 2 and 3 when as yet they were not culturally diversified, and no. 2 helped no. 1 forward, it being easier for plants to spread east or west than north or south against the influences of heat and day-lengths. China did much independent originating, the results of a struggle of a peculiar people against a peculiar climate ; India and Indo-China owed their differences to India coming under the influence of south-western Asia, whereas Indo-China was out of reach. Malaysia and the Pacific as laggards differ in degree from the last named. But the corner-stone everywhere was in what Nature gave for Man to use, and the first advance was made possible by pre-existing pastoralism. On realizing this, I was somewhat disturbed by the fact that there are pastoralists in Asia who refuse to till, for instance Mongols whose complete refusal to add anything to their food of a vegetable nature seemed to deny that a pastoralist must start tilling when to do so is easy. There are abundant references in print to this Mongol habit ; yet doubting their verbal accuracy, I consulted Dr. Joseph F. Rock who has travelled among the Mongols. I asked if his Mongols disregard the easy possibility of flavouring their mutton from the abundant wild species of the genus *Allium* on their lands, to which Dr. Rock said that they do not even use these. But again it is not the whole of the Mongols who refuse to cultivate. Rysanovsky records in his *Customary laws of the Mongol tribes* (1939) that among some of them provision is made for resuming possession of land tilled in the previous year ; i.e. they till at times. I conclude that where riches are in the flocks, pride makes the richer ostentatious in not tilling.

There are no grounds on which it is possible to name one particular cereal as the first that Man adopted ; but these as alternatives assuredly came through the first trials and were established early—the ancestry of the cultivated Barley (*Hordeum vulgare*), the Small spelt (*Triticum monococcum*), the line of the Wheat beginning with Emmer (*Triticum dicoccum*) or something like it, the Common millet (*Panicum miliaceum*) and the ancestry of the Foxtail millet (*Setaria italica*). Vavilov on his differential theory says that Emmer took origin in Abyssinia and the two millets in the Far East. The statement is a declaration of their great variability in the places named ; but it is easier to think that Abyssinia and the Far East received these crops than that they originated them.

Barley, when 2-rowed, has an obvious parent in the wild *H. spontaneum* C. Koch, which grows in Palestine, Syria, Mesopotamia, Persia, Turkestan and Afghanistan, i.e. in the compartments of the Near East and Inner Asia. It is completely interfertile with *H. vulgare*. Barley, when 6-rowed, could have come from *H. agriocrithon* Aberg, which apparently is not rare in Tibet and extends towards Turkestan, and may possibly be the 6-rowed wild plant reported from Transcaucasia. Thus there is a home for Barley where expected. When were the parents taken into cultivation ?—the one or the other in time for the cultigen *H. vulgare* to have been made and spread before c. 6000 B.C., by which time it had become a crop of the Nile valley and Mesopotamia. This date

is more or less that of a burial at Silsile, which is a fair way up stream from Thebes (Schweinfurth in *Wissensch. Veroff. d. Deutsch Orient Gesellsch.*, 8, 152, 1908), where it was found, as well as of ruins in Nippur in Babylonia. Written records show Barley to have been the chief grain of Sumeria in the 3rd millennium as it was of Upper Egypt. The grain was eaten either as porridge or as torrifried groats.

Emmer (*Triticum dicoccum*) is sufficiently like *T. dicoccoides* Koernicke, to have been derived from it; and if so, would have been originated within the area—Palestine, Syria, Mesopotamia, Persia and Kurdistan, where *T. dicoccoides* is wild: this is contrary to Vavilov's theory of an Abyssinian origin. It was found with Barley in the Silsile burial; and it became so much the leading cereal crop of Lower Egypt that the harvest month was named after it. Barley and Emmer were possibly in equal demand in Egypt until the device of bread making towards 2000 B.C. threw Barley into the background.

The Small spelt (*Triticum monococcum*) occurs wild through Asia Minor as well as in the Crimea. Being second class, the better grains named above seem to have blocked its extension towards the south and south-east; but its cultivation spread north-westwards into Europe.

The Foxtail millet (*Setaria italica*) is regarded as a cultigen derived from *S. viridis* Beauv., a grass of very wide dispersal from the Atlantic right across Europe and Asia. It would not be unnatural for Man to have taken the parent into cultivation in more than one part of the area, for he took into cultivation other species of *Setaria* in various places and ennobled them in a less measure; and origination in Inner Asia as one of the several is quite probable. Vavilov and Bukinovich discovered that in Afghanistan today the grain of *Setaria viridis* is harvested (*Bull. appl. Bot. suppl.*, 33, 545, 1929).

The Common millet (*Panicum miliaceum*) has the same climatic requirements as the Foxtail millet which, considered along with their very general companionship, suggests origination in the same part of the world; but no parental form has been proved. The nearest form is the Abyssinian *P. callosum* Hochst.; and this might as easily be a derivative as otherwise. Vavilov is by no means the only botanist who has claimed an origination for it in the Far East; but origination in Inner Asia would afford a better centre from which it could be dispersed. We know of it in cultivation in Europe and in China alike at early dates.

The Millets are crops of shorter duration than the others. No one prefers them. Grain of millet is 'arzan' in Persia where 'arzani' means cheapness. Not long ago and possibly still, the grain was sold in Turkestan at only two-thirds of the price of wheat. The Russian soldier in Siberia is provided with it as rations because it is cheap. The poor in Peiping abandon the eating of it immediately they can afford a better grain. So from early days would Man tolerate it where the seasons or his habits demanded an early return; and I cannot but think that the opportunities of Inner Asia favoured millets when those of Near Asia favoured Barley, Emmer and later the better Wheats.

When in 250 B.C. the Babylonian priest Berosus wrote that Barley grew wild in his country, he may have had *Hordeum spontaneum* in mind. When Pliny wrote that Barley was the oldest (antiquissimum) of the cereals, he doubtless was echoing a popular belief. It was ancient anyhow; and to be already 'barley' by 6000 B.C., the wild parents must have been taken by Man up to a millennium earlier.

It is easy to match pulses against the cereals named as the first of the Near East and Inner Asia; these come to the mind at once—the Chick pea (*Cicer arietinum*), the Garden pea (*Pisum sativum*), out of which the Field pea (*P. arvense*) is a development, the Broad bean (*Faba vulgaris*) and the Lentil (*Lens culinaris* Med., or more familiarly *L. esculenta* Moench.). The Chick pea had for its parent *Cicer pinnatifidum* Jaub. & Spach, which grows wild in

Palestine, Syria and Asia Minor (see Popov in *Bull. appl. Bot.*, **21/1**, 1928). The origins of the others are not so straightforward. The Lentil has been originated in more than one centre. It is found wild in Asia with small seeds and wild in the Mediterranean with large seeds (the subsp. *L. macrosperma* of some writers). De Candolle regarded the latter as large seeded by ennoblement and wild by escape. On that view he could postulate a single centre of origination, namely the Near East. Barulina in a very elaborate monograph (*Bull. appl. Bot.*, **40**, 1940) gives as her view that the large seeded came into cultivation from a wild state in the Mediterranean. The difference in size of seed can be remarkable: Vavilov took samples of 100 seeds from Spain, Algiers and Italy which weighed respectively 9.0, 8.8 and 8.3 grammes, whereas similar samples from Bokhara, Afghanistan and India weighed respectively 2.6, 2.5 and 2.0 grammes. The greater antiquity of tillage in Asia would indicate the first centre to be in Asia; and Barulina suggests on Vavilov's differential method, northern Afghanistan for the centre of origin, regarding which I would say that it is evidently very well suited to the climate and variable because it is carelessly cultivated. It is cultivated from the Atlantic to the Pacific, far beyond the area that can have been natural to it wild. Hehn shows on linguistic ground that the Lithuanians and Slavs received it from Italy and that in Asia it was passed northwards from Persia, for the Persians did not know it until they moved into Persia. Barulina points out that the plant shows many races in Greece, Italy and Spain.

The Garden pea originated in south-western Asia; but its parentage still needs analysis. Govorov (in *Bull. appl. Bot.*, **19/2**, 1928) suggests three lines of ennoblement which he calls *Pisum sativum*, *P. arvense* and *P. asiaticum*; but that this makes discussion of its origin easier or not is conjectural. He finds a differentiation centre for all three in Afghanistan and a minor centre in Abyssinia. As in the Lentil, so here the races of Asia are smaller seeded than the races of Europe.

The Broad bean is the most intriguing of all the cultivated Leguminosae. De Candolle discussing it with great care (*Origin of cultivated plants*, p. 316, 1884) was reduced to suggesting that a parent, at one time spread from the western Mediterranean to the Caucasus and northern Persia, had failed to hold its place save at the two extremities, so leading to a doubled ennobling. Whether this suggestion be accepted or not, Man has been able to cause the Mediterranean line to have strikingly large seeds, while the asiatic line has small seeds; and the seeds of the Mediterranean line are no longer pulse, but are eaten before maturity as greens. Vavilov gives these figures of the sizes of the seeds (*Bull. appl. Bot.*, **16/2**, 129, 1927), 100 seeds from Spain, Tunis and Italy weighed respectively 200, 171 and 130 grammes against the same number of seeds from Bokhara, Persia and India, 38, 30 and 20. He found his differentiation centre in Afghanistan (*Bull. cit. suppl.*, **33**, 578, 1929).

I would mention yet two more pulses, the 'Kesari' of India (*Lathyrus sativus*) and the French lentil (*Vicia ervilia*). The first is the cheapest pulse of India where it appears as a weed in Barley crops in a way that seems to illustrate how pulse cultivation began. Vavilov suggests that its home is Afghanistan; De Candolle had suggested the country south of the Caucasus and Caspian. The other pulse, *Ervum ervilia*, is particularly a crop from the Caucasus to Afghanistan; and its use in Spain is a result of the Arab domination which began in A.D. 711. Campbell Thompson suggests that it was the 'se-sis' of Sumeria (*Dict. Assy. Bot.*, p. 102, 1949).

It is rather difficult to point with confidence to the plants that were in demand as 'greens' among the first cultivators. This class, 'greens', covers all plants that supply from vegetative parts above ground, tender tissues, such as young leaves and stems, young fruits and immature seeds; and the sources are exceedingly numerous. Ochse (*Vegetables of the Dutch East Indies*, 1931)

enumerates 298 species whose leaves are eaten in Malaysia, chiefly in Java, mostly when very young. When alternatives are so numerous, and supplies are available from wild plants, where is the inducement to cultivate? Early Man would be in no haste to extend his small plots if the open field satisfied his needs; but in a curious way suspicions are aroused that some of the greens of the Near East were not taken into cultivation as greens but as oil-seeds. The Lettuce is among them. It is generally accepted that the cultivated Lettuce (*Lactuca sativa*) had its origin in the Near East from *L. scariola* L. But no one cultivates the latter for the sake of its leaves; however, it is a subordinate oil-seed today in parts of Africa. If we infer, as is reasonable, that when the origination of the Lettuce began, and its parental form was cultivated, then it was cultivated for its seeds.

The Cress that we eat in 'mustard and cress' is from an oil-seed plant (*Lepidium sativum*) of the same part of the world. Brassicas store oil in their seeds and the young leaves can be used as greens; the oil might well have been the cause of their cultivation. There is no natural connection between carrying oil in the seed and producing an abundance of leafage; but cultivation pointed in the two ways and the oils are edible oils.

Spinach (*Spinacea oleracea*) and the leafy Beet (*Beta vulgaris* var. *cicla*, or near it) entered into Man's tilled plots in this part of Asia. High temperatures force Beet into flowering; lower temperatures lead to over-wintering with a swollen root. Spinach and the Beet are sufficiently alike to have had their names confused when they were transmitted eastwards (see for instance Laufer, *Sino-iranica*, p. 395, 1919) which would not have happened if the root-forming Beet had been transmitted. Laufer thought that the leafy Beet had been carried to China by Arabs; and if so, they, sailing from Persian ports would have the leafy Beet. A leafy Beet diffused into India where Roxburgh, finding it, called it *B. benghalensis*. Endive (*Cichorium endivia*) and Chicory (*C. intybus*) were ennobled, the last partly, in the Near East; and Endive seems to have furnished the 'bitter herbs' of the Jewish Passover. The Cucumber (*Cucumis sativus*) and the Melon (*C. melo*) had ennoblement also: there would be a time when the Melon had not become sweet.

I turn to the genus *Brassica*, great in the service of Man for its seeds, its leaves and its swollen tuberous stems or roots; and again as the Cauliflower for its inflorescences. This polymorphy is associated with chromosome dissimilarities; and the interspecific sterilities resulting, by means of the isolation of species that they produce, have been invaluable to Man in his work of ennobling.

Raphanus, without chromosome dissimilarities, serves Man like *Brassica*, yielding oil, greens and roots, but without the striking polymorphy. *Camelina* and *Eruca* yield oil and greens.

I think it significant that the two Brassicas which particularly supply greens are at home where they get sea winds, *B. oleracea* by the Atlantic and *B. chinensis* by the Pacific. The place of *B. juncea* is midway; and it is the most tropical; and as such is rather wide-spread in Africa. It is pungent in its wild states as a defence against herbivores; but a double boiling enables Man to remove enough of the pungency for use as food; and, submitting to that extra trouble, he has found it worth while to enoble it in south-western Asia. It has the chromosome number, $n=18$, and meeting *B. chinensis* which has the chromosome number, $n=10$, the two could not cross; and *B. juncea*, diffusing eastwards into the country of *B. chinensis* has been accepted greedily by China and grown without confusion with *B. chinensis*. *B. chinensis* meanwhile has been broken (imperfectly) into the microspecies *B. subsp. chinensis*, *B. pekinensis* and *B. nipposinica* which so freely intercross that it is only by Man's action that they are kept apart. On the western side of *B. juncea* the arrangement of 10 chromosomes is met with again, the closely allied species, *B. campestris* and *B. rapa*, having it. It is

evident that they had a common origin and that it was on the less tropical side of *B. juncea*, for *B. campestris* extends as a wild plant into Siberia.

The early cultivators must have been considerably favoured by Nature's imposition of the isolation preventing crossing with *B. juncea* and it has to be added, with *B. napus*; for the chromosomes in *B. napus* are $n=18$, as in *B. juncea*. The separation of *B. rapa* from *B. campestris* must be attributed to Man. De Candolle wrote "when the root or lower part of the stem is fleshy, the seed is not abundant": I am uncertain if that is so pronounced that Man, finding his seed-crop diminished when he ennobled for roots, would be led into the channels dividing rape from turnips; but it might be so. The diverging must have been started in south-western Asia and both lines found their way through *B. juncea*, diffusing independently towards the East and producing these two parallels: (a) while the rapes were being brought forward in the West and being worked up into a line which today ends in 'Colza', working up in the East was leading to the 'Sarson' of India and its like; (b) while the turnip was being brought forward in the West—brought forward early and so effectively that Pliny could write that it came third in importance in Italy after the vine and corn (18.127)—in Asia eastern turnips were getting character and, thanks to their cold-resistance, a comparably important place; turnips, for instance, are today the winter vegetable of Tibet. When they reached China, it would be found that they crossed with *B. chinensis*, but Chinese horticulture was on their arrival efficient enough to see to that.

In Europe the possession of Turnips did not preclude ennoblement for tubers of *B. napus*, nor did it in the East; for in the West the Swede was extracted and in the East the Pak-choi (Bhutia rai of the Himalaya). South-western Asia seems to have been the eastward limit of the area over which *B. oleracea* developed; but its chief ennoblement must have been in the Mediterranean and within reach of the Atlantic winds. Pliny wrote of cabbages heavy enough to break a cottager's table: I should like to know if the enormous cabbages reported from Manchuria (see for instance Hosie, *Manchuria*, p. 196, 1901) are produced by the favouring of winds from the sea.

The Radish (*Raphanus sativus* L. sensu latissimo) is of so many forms that taxonomists easily devise subspecies and discover ways in which demands can be met that parents should be forthcoming in lands from the Atlantic to the Pacific. As in *Brassica* so in *Raphanus*, ennoblement has resulted in oil and tuber being alternative objectives. Europe, at one time found the oil worth producing, but does so no longer. Europe at one time was interested in raising bulky radishes for food, but now uses little radishes for their condiment value. The bulky radishes hold their place firmly in tropical Africa, India and China; and the leaves serve as greens. Such must have been the Radish which Khnema Khufu, the Cheops of Herodotus (ii. 124), supplied to the workmen who built his pyramid, the greatest pyramid in Egypt, c. 2780 B.C. The record indicates an importance like that which Pliny attributed to the turnip in Italy nearly three millennia later. The origination of this certainly bulky radish must have been in the Near East and nearby part of the Mediterranean; and the latin name 'radix syria' was an appropriate one. The Japanese microspecies *R. raphanistroides* Sinsk., has had its origin in a Japanese wild form.

The Near East and the Mediterranean together have provided four other related sources of oil, *Brassica nigra* Koch, *Sinapis alba* L., *Camelina sativa* Fries and *Eruca sativa* Lamk. It is interesting that Man found Nature to provide all these in the one part of the world just as she provided him with a group of cereals in another part, but not really surprising that he should adopt for use a group at a time, and sort them out later in tillage.

The dwellers in the Near East came to demand oil in considerable quantities. The records of production-control by Assyrian and Babylonian kings and, later, of the maintenance of public baths in the cities and towns where all comers oiled themselves profusely, suggest that the land could not produce enough.

Sesame (*Sesamum indicum*) and the Castor-oil plant (*Ricinus communis*) seem to have been welcome when they reached the East. The latter was already in Egypt in the time of the Badarian civilization (between 4000 and 3200 B.C.) and three millennia later Herodotus found its oil to be used as an unguent in the marshes of the Nile (ii. 94). Sesame had reached Sumeria by the time of the 3rd dynasty of Ur (say c. 2350 B.C.), and is recorded as 'se-gis-mi', after which date it becomes of frequent mention in the clay tablets that have been read (see Campbell Thompson, *op. cit.*, pp. 98, 101). The Castor-oil plant, very variable in Africa, has either varied since arrival in Europe and Asia or there have been introductions of variety after variety. Persia holds a curious small seeded form.

The several valencies of the Brassicas—for greens, oil, tubers—have carried my narrative away from greens to oil-seeds, but I return to give a place to the Onion (*Allium cepa*) which combines the qualities of greens and condiment and is the best of a group of greens with alliaceous flavour. The genus *Allium* extends from the Atlantic across Europe and Asia, south to Abyssinia, and is in America. Garlic, Leek and Chives are all traced with ease to wild sources, but not the true Onion, which seems to have been brought to the Near East from deep in Asia. A cold spell is good for it and flower-formation needs long daylight; its home moreover had droughts, for it guards itself against them. It would get these conditions in, say, Dahuria which is regarded as the home of Chives (*A. fistulosum*); and we may assume that it was brought out of Inner Asia to the Near East where first we hear of it. Khnema Khufu supplied it to his labourers along with the radishes and garlic (*A. sativum*). The Leek (*A. porrum*) has been proved in Assyria from about 1950 B.C. (Campbell Thompson, *op. cit.*, p. 52); but all these species had undoubtedly been already long in cultivation.

There is a little interest to be got regarding fibre plants by reading Herodotus' account (vii. 631) of the way in which the contingents in Xerxes' vast army were clad when Greece was invaded by them in 480 B.C. Nearly all of them were clad in skins; only the Assyrians were in linen and the Indians in cotton. The cotton bush had been brought to Assyria by Sennacherib about 694 B.C., but had not displaced linen.

The Cotton bush is the first woody plant that I have had cause to name in this gathering together of the early assets of south-western Asia. The Bible frequently refers to 'the field', meaning the agricultural land which was not fenced, and then again to the orchard which was fenced. That conveys a distinction between the herb and the tree, and it, indeed, relates to two distinct cultivation techniques: in the field the plant was sown and the harvest was gathered en masse; in the orchard the individual was treated as such, was planted by itself and was propagated in a very large measure asexually. This had two results: Man learned much about the ways of life of his woody plants, but lost a large proportion of his opportunities for selection through seed: his best chance of advance with trees was by search in the countryside for something that Nature had to give that was better than what he already had, and to take it into his care. Apart from the intensity of the search, he was in the position of advancing more slowly with the woody than with the herbaceous plants: we can extend beyond the word woody and say "more slowly with the perennials than with the annuals".

Possibly the Fig (*Ficus carica*) was the first tree to be cultivated in the Near East and it is likely that Man obtained more horticultural skill by attention to it than by anything else. It was manifestly very well adapted for experiment; but it is useless to guess when he began with it.

While the Syrian was practising grafting fig trees, his neighbour to the south was multiplying the Date palm by suckers from ground level and learning that they in time gave fruit exactly as the parent. Both Syrian and Arabian were making curious discoveries in pollination which I must pass by. Then wine-making was invented in south-western Asia which brought the Grape-vine (*Vitis vinifera*) from the position of a forest fruit to be had in season to something

to be raised in quantity ; and it was amenable to multiplication by cuttings. It is significant that when the knowledge of wine-making came to the Greeks they said, " we have that plant and call it *ampelos* " and when it came to the Latins, the Latins made the same remark substituting '*vitis*', with the same meaning as *ampelos*, twiner (Thiselton-Dyer in Whibley's *A companion to Greek studies*, p. 61, 1916). And wine-making brought the Grape-vine within the orchard fence.

I have tried to show that Man owed the locality in which he initiated tillage of cereals to Nature's offer of proper materials ; and I wish to show that the generosity of Nature led to the promotion of fruit-culture in the same quarter. Vavilov has written enthusiastically of the richness of the forests in the Caucasus and the Kopet Dagh in woods wholly of wild pears and apples or of other trees that could be parents of most of the European fruit-trees. These inviting regions are not remote from Mesopotamia. Sargon of Akkad who reigned *c.* 2870, made an expedition over the Taurus and brought back desirable trees (Woolley, *The Sumerians*, p. 79, 1928). Queen Shub-ad of Ur was buried (before 2600 B.C.) in a bonnet adorned by models in gold of pears and pomegranates ; and no doubt there was a lively interest in cultivating desirable fruit in the Euphrates plains in the 3rd millennium B.C. from times before. Later, so we read, Menush, a king of Haldia (near Lake Van, Kurdistan) conducted water by a canal, planting its margins with fruit-trees ; and we are told of the tree-plantings of great Assyrian despots of the 8th and 7th centuries B.C., Tiglath-Pilezer, Sennacherib and Ashur-bani-pal ; and there is a despatch in existence of Darius, son of Hystaspes, King of Persia 521-485 B.C., to an official named Gadates stationed among the Greek colonies in Asia Minor, congratulating him on his " care of the plants from beyond the Euphrates ". Xerxes, the son of Darius, and Cyrus, the claimant of the Persian throne in 401, were also great tree planters. They had not been, if the material had not been handy in the country to their north. Nature had so worked there that many trees had water-storing tissue about their growing ovules, which, when the ovules had finished growing, could be used to promote seed-dispersal ; and the trees with that purpose had given origin to fleshy fruits of which a rather striking assemblage was available. It rested for someone to explore it ; and the kings about Mesopotamia were induced to do that.

Their fruit-trees had become well distributed in the Near East when the Romans needed to send administrators to govern the lands surrendered to them on the overthrow of Mithridates (66 B.C.) ; and the administrators took a pride in bringing some of the fruits to Rome. At this time Varro said Italy had become an orchard. Though Darius was master of a part of India and Xerxes drew troops from India, no Indian fruit-trees are known to have been brought by the Persian rulers to their own country.

In central Europe " we find everywhere evidence of the arrival towards 4000 B.C. from the East of a short-headed race and of human settling through the forest region on the sides of lakes and steppes which expose the first signs of agriculture and pastoralism " (Kern in *Arch. Rassen u. ges. Biologie*, 22, 199). All that the settler grew is not demonstrable ; but very patient study of old inhabited sites in Switzerland and elsewhere enables us to name plants grown in the 3rd and 4th millennia by identification of their seeds from the mud. A convenient list of them is in Dr. Elizabeth Schieman's *Entstehung der Kulturpflanzen* (pp. 22-23, 1932). Most of the identified seeds are of wild plants, natural to the neighbourhood ; a minority were cultivated. Barley was grown in three forms ; Wheat in three forms, Emmer and Small spelt and the two millets, *Panicum miliaceum* and *Setaria italica*, the Broad bean, the Pea and the Lentil. Of Apples there were two sizes, and it has been suggested that one of them was cultivated, though that seems questionable. Excluding the Apple all the cultivated plants were annuals.

It is somewhat astonishing how little we know of contemporaneous cultivation in the Mediterranean region. Agriculture there was, and trade which carried metal tools about. From Coon's *Races of Europe* (1939) I have borrowed a map of the spread of metals, which he zoned in half-millennia, and I have ruled on it an arrow to indicate the migration of the round-headed folk who brought the first signs of agriculture. This line is beyond the area of contemporaneous use of metals. It is proved that Emmer was the cereal of Italy in the 2nd millennium B.C., and as just mentioned, it was a cereal of the Swiss lake dwellings in the 3rd millennium. The curved line on the map is the suggested course by which Emmer reached the Swiss lakes, Greece being off it. Greece is a country poor in corn land and indeed imported corn in classical times, paying for it in wine and oil; and if Greece had Emmer early, it was probably obtained from Thrace, where, as probably also in the Swiss lakes, it had been preceded by millets. At 400 B.C. the classical Greeks were very well

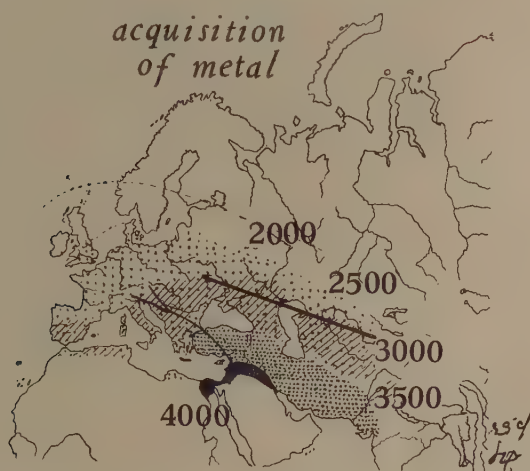


FIG. 5.—Europe zoned in half-millennia by the spread of metals, with an arrow to indicate the direction of the movement of the round-headed migrants from Asia to central Europe to show that their course would be neolithic; and with a second line suggesting the diffusion of Emmer from Syria to central Europe.

aware of neighbours towards the north with a way of feeding unlike their own; they being the Scythians who fed on millet; and the habit seemed to the Greeks strange enough for comment. Xenophon, returning with 'The ten-thousand' recorded falling in with it at the western end of the Black Sea. Herodotus, home from Babylon, told his countrymen (iv. 17) that Scythians and their neighbours on the north of the Black Sea, though they had wheat (this would be Emmer) ate millet. The attitude of the Romans towards the millets was like that of the Greeks; they looked down on millet-eaters and knew the Gauls to be such, but it happened to be a Greek who recorded this—Polybius, carried to Rome as a hostage in 167 B.C. and sent with the other hostages taken at the same time to the Etruscan frontier next to the Gauls, though later allowed to reside in Rome. He tells that with his own eyes he had seen an abundance of millet and that the Trans-alpine Gauls grew it likewise. Julius Caesar sent a lieutenant, Tribonius, to besiege Massilia (Marseilles) in 49 B.C.; and it is recorded that the garrison was reduced to feeding on old millet and spoiled barley. Strabo, the

geographer (56 B.C.—A.D. 24), recorded that the Iberians of France, living between the Garonne and the Pyrenees, raised millet as their universal grain. These references show that crops of it bordered the Mediterranean within which it was refused ; but better grain was diffusing through the millet and Julius Caesar had no difficulty in getting in Britain on his first visit (55 B.C.) the corn that he demanded.—Thereafter the Romans insisted on Britain raising wheat and supplied it to their armies on the Rhine. I have mentioned earlier that no one eats millet by preference to wheat ; but cultivators may be obliged by climate or their own habits to grow millet rather than wheat, and the millet belt about the Mediterranean must have existed by the cultivator's will, say by his reaction to something in the climate, for the only part of Italy where millet growing ruled has the climate of central Europe.

It we allow that it was the migrants from the East who brought millet-growing, then the presence very early of *Cannabis* in the soil of the Upper Danube is a sign that they brought it also. The Garden pea, the Broad bean and the Lentil, demonstrated to have been in the possession of the dwellers by the Swiss lakes, could have travelled as Emmer probably did. Having reached the edge of the Alps, these were in a position to descend Italy and do this long before there was shipping enough to annul the Adriatic as a barrier. This came about towards 750 B.C. A little earlier Carthage had been founded, and the Phoenicians in time took to the western Mediterranean the plants that Syria had. They took, for instance, the Pomegranate which became 'punica' in Latin because Italy received it via Carthage. Cato, trying to drive the Romans to make war on Carthage, held up in the senate a fresh fig with "see how near our enemy is that we can obtain this from him". And the Grape-vine was established in Morocco with great success. There was written a book on the agriculture of Carthage which is lost, and there is no knowing what more they took ; and it was left to the Syrians serving under the Arabs after Spain was invaded in A.D. 711 to cultivate many eastern plants in Spain which they knew there under Arabic names.

The Sugar-cane was brought by them in A.D. 714, and probably *Colocasia esculentum* (see *Proc. Linn. Soc. Lond.* sess. 150, p. 85, 1938). Both of these had had to travel from India to Syria and Egypt and had reached the eastern Mediterranean about the beginning of our era. The Egg-plant (*Solanum melongena*) and the Carob (*Ceratonia siliqua*) were others.

Sir William Thiselton-Dyer did a great service for my subject when he made compendia of all the economic plants referred to in the Greek and the Latin classics. The first was published in Whibley's *Companion to Greek studies* (pp. 42–68, 1916) ; the second in Sandys' *Companion to Latin studies* (pp. 66–89 of the revised edition of 1921). The frugality of the Greeks, as he comments, caused every possible native plant to be used as food, and an insipid herby diet demanded an abundance of condiments to help it down. The Greeks resorted to the Onion firstly but, besides, to many Labiates, Cruciferae and Umbelliferae, such as were readily obtained from the fields, and if brought into cultivation were only slightly ennobled. In Italy there was likewise an extensive diet of greens. Horace mentions boiled mallows and boiled nettles. Other herbs supplying spinach-like dishes were *Valerianella olitoria*, Purslane (*Portulaca olitoria*), Alexanders (*Smyrniolum olusatrum*), *Eruca sativa* and species of *Rumex* which have not or have scarcely been ennobled.

The Roman walled-in garden held greens that were better but had not come from far away :—Leek, Cabbage, Sea-kale, Chicory, Globe artichoke, etc. Thiselton-Dyer remarked that the Mediterranean had made its own greens.

The Roman occupation of Gaul brought about a head-on collision between the indifferent cultivation of the Germans, with their millet, and the Roman cultivation. The Romans compelled the Germans to raise their own resources, taught them to eat cabbage and take to many southern herbs. It is only necessary

to scan the following list of plants of German gardens with names in German from the Latin to see this: the Garden pea, Lentil, Parsley, Onion, Beetroot, Caraway, Radish, Horse-radish, Mint, Coriander, Chervil, Lovage, Lavender, Penny-royal, Lettuce, Fennel, Aniseed, Asparagus; and, says Hehn (*op. cit.*, p. 494), after naming the above, with their origins, 'there are many more'.

In so far as it is reasonable to believe that millet-growing was brought from Inner Asia to central Europe, it is reasonable to ask if it could have been taken in like manner from Inner Asia to northern China. An early importance of millets in northern China is proved in various oblique ways. The reputed founder of the Chou dynasty (1122 B.C.) is given a name which is millet deified. The oracle bones excavated at An-yang (for its position see fig. 4, p. 19) ask if the millet crops will be good, the period being late in the 2nd millennium B.C. The ancient ceremony, the origination of which is attributed to Shen-nung (2737-2705 B.C.), of sowing Five Grains is usually found to include the millets as two of the five; but apparently there was greater sanctity in the number being five than in their precise nature. A demonstration of the continuing in favour of millet lies in the great value put on the millets still by the thousands of Chinese who live from hand to mouth. The Great millet or Kao liang, a species of Sorghum, was not in China then. I think that the original two millets reached China very early from Inner Asia and were extensively ennobled in China. I do not add the following as proving how they came, but call attention to Baron von Richthofen's theory that the Chinese had come into their country from Khotan, that is by the way in which the Millets could have come.

As the soil of An-yang has provided Hemp seed; and as *Cannabis sativa* is a native of Inner Asia, so its presence along with millets suggests the millets' travelling.

When the Chinese started cultivating for cereals, there was an indigenous pulse, *Glycine hispida* Maxim., volunteering in their fields, ready for adoption as a crop which indeed it became and, ennobled to *G. soja*, proved so satisfying that its name in Chinese came to mean pulse.

The Chinese received other cereals and pulses from south-western Asia before there is any record of their travel, for it cannot have been long before they had Wheat and Barley, the Broad bean, Garden pea and Lentil. It has been suggested that they received Rice from the south at a very early date, the evidence being the pitting of the surface of an old piece of pottery (see Anderssen, *Children of the Yellow Earth*, p. 186, 1934); but it is difficult to accept the dates he puts forward. Among the bones unearthed at An-yang are in small number those of the Water buffalo which in domestication is the beast of heavy ploughing as in water for Rice; but it were rash to insist on the possession of Rice from the possession of the buffalo.

The centre of Asia bred nomads; and they hemmed in the Chinese on the west and, moreover, preyed on them. The sea confined the Chinese on the east, and adventurers to Japan merely added Japan to the area of Chinese economy without making room for Chinese. They tried expansion northwards into Ordos, but could not feed their colonists. The only opening for them was an overflow southwards. This considerable confinement resulted in the agriculturally very efficient Chinese developing autochthonously—not so much at the cereal or even the pulse level, as from the greens level of the sequence (see p. 14). The originality of the development was consequential on the very unkind climate of the northern spring, at which time very cold and very dry winds sweep down from the Cold pole in eastern Siberia and prevent the renewal of growth in the vegetation, while an enduring grey dust-storm shuts the sun out. At 1000 B.C. the Chinese were fighting their way southwards. At 600 B.C. they had crossed the Yang-tze kiang, having already the stamp of originality deeply impressed on their feeding. As they advanced southwards they absorbed the crops of a less unkind climate in a degree that makes 600 B.C. the end of an epoch.

The Chinese had taken to eating seedlings, as we in spring eat 'mustard and cress', chiefly those of their pulses. The Soya bean is one; others that they eat today include the Broad bean, *Vigna sinensis*, *Phaseolus aureus* and other species of that genus; then outside the pulses, seedlings of the Labiate *Perilla ocimoides*, of the Composite *Aster indicus* and of the Polygonaceae of both species of *Fagopyrum*; there are others. I was astonished to observe in the central market in Shanghai how much of the Shepherd's purse (*Capsella bursa-pastoris*) and *Medicago denticulata* is consumed; but these are not cultivated plants: I introduce their names only to illustrate the intensity of the need in March for any form of edible growing stuff. Of cultivated plants they eat large quantities of the new shoots of *Chrysanthemum* as we eat Brussels sprouts; and bulbs of *Lilium tigrinum* and allied species.

In the spring-time of the year before the Japanese spring festival has come, the Japanese make use of the petioles and new leaves of *Petasites japonica* and *Oenanthe stolonifera*, the tender shoots of *Aralia cordata*, which plants may be called semi-cultigens, and of *Alliaria wasabi* (*Wasabia japonica*), a not unpleasantly pungent vegetable.

The East has done its utmost to make *Brassica chinensis* into the best of cultigens and split it into several microspecies only held apart by cultivation-methods: I have already made some remarks on them (see p. 23).

Nothing proclaims the originality of Chinese agriculture more than their resort to silk as a fibre. They possibly adopted *Abutilon avicennae* as their first fibre plant, and silk, a luxury fibre, not until long after, when they were already cultivating the Mulberry and many fruit-trees. The excellence, today, of certain of their fruits shows that they developed much horticultural skill, which they applied effectively to the Persimmon (*Diospyros kaki*), the Jujube (*Zizyphus jujuba* Lamk.), the Peach (*Prunus persica*), the Apricot (*Prunus armeniaca*) and the Walnut (*Juglans regia*). The Chinese were fruit-tree-minded before the Latins, but apparently not before the people of south-west Asia to which the Peach and Apricot may have extended naturally and in which these two were brought forward as well as in China. The earliest record of the cultivation of a Chinese fruit-tree is Mencius' undoubtedly late mention of the Mulberry in "happy the peasant in possession of a few mulberry-trees about his dwelling that he may clothe his parents in silk"; for Mencius died in 289 B.C. We must allow to silk a long earlier development; and in 325 B.C. something was known of it in India which reached the ears of Nearchus, there with Alexander-the-Great. It seems that about this time silken robes were carried out of China as gifts to the great. In 134 B.C. the Chinese emperor sent his general Chang Kien westward to seek out the wandering Yue-chi Mongols and to make a treaty with them against a common enemy, the Hiung-nu; and when the general came back after ten adventurous years with seeds of the Grape-vine and of Alfalfa (*Medicago sativa*) it was to tell his master that a great trading nation could be reached in Inner Asia by taking the road by which he went. The emperor made use of the Grape stones to plant a vineyard about one of his palaces, and the coming of the Grape to China added a borrowed word to Chinese, for their wild grape went nameless (see Laufer, *op. cit.*, p. 225) and was now named after the cultivated vine from the language of Ferghana. This recalls what happened in Greece and Italy on the coming of wine-making (see p. 26). The bringing of the Alfalfa seeds shows that it had been in the general's mind to improve the breed of horses that China had, for alfalfa had become the standard horse fodder and it actually reached Italy for the purpose in the time of Chang Kien. China must have been very ready to trade, as in the next few years after this caravans to the number of twelve a year went over the Silk road, as the way came to be called, often ending the journey at the Ferghana annual horse fair. Herrmann (*Die alten Siedenstrasse*, p. 3, 1910) suggests that though it is uncertain that from the very first they set out carrying silk, this very soon became their chief outward merchandise.

About fifty years ago, I happened to need some transport animals close to the Burma-Siamese border and was able to hire them from Chinese traders making annually a journey from Yun-nan to Tenasserim; they traded all the way but the only thing light enough for through carriage was silk. I mention this to call attention to its great suitability for the nascent China-Inner Asia trade.

A sequel to the honours which fell on Chang Kien was that the Chinese took to crediting to him the introduction into China of any western plants the original bringing of which was hidden from them. Laufer in his *Sino-Iranica* set himself the task of disproving statements that Chang Kien had brought into China Sesame, Coriander, the Pomegranate, a Cucumber, Chives, Safflower, a Fig and a Walnut. The direction, however, whence they came, except possibly the Walnut, was correctly assumed as the Silk road. It seems that the habit of attributing these to Chiang Kien grew about 400-500 years after his death, and the date of their coming, when the necessary allowance for loss of record is made, might be regarded as about the 1st century A.D. We then observe that a fruit-tree such as the Pomegranate soon had more than one race in China: we detect repeated introduction as indeed must have happened. The fruit of the Pomegranate is perfected for transport. Did northern China receive Sorghum over the Silk road? This needs working out.

It suits me to return to south-western Asia, for besides Sorghum there are African plants such as Sesame whose advent in China needs explanation. It has already been mentioned that the Near East seems to have welcomed the coming of Sesame, being greedy for more and more oil-seeds, and that its name appears in Sumerian records about 2350 B.C. Though the way to Sumeria is not documented, Strabo (c. 54 B.C.-A.D. 24) states that it was the oil-seed of southern Arabia in his time (xvi, 4, 26), and proves its fitness for the climate. It is interesting to observe the length of time—nearly three millennia—that it took to reach northern China. I wish that one could apportion that time between slowness due to Man's direct passings forward, and slowness demanded by acclimatizations.

The African genus *Vigna* supplied *V. sinensis* to Asia over the Sabaeen lane, as Schweinfurth suggested (*Verhandl. d. Berlin. Anthrop. Gesellschaft., Sitz. v. 18 Juli, 1891*). Campbell Thompson has found its name as lu-ub-sar (the parent of the modern Arabic 'lobia') in Sumerian records of about the same date as Sesame's. The Greeks accepting this plant and intrigued by the vexillum and keel of the flower, renamed it 'phaselos'.

Sorghum certainly came along the Sabaeen lane, not once, but many times, possibly incessantly in use as a viaticum. Naturally the microspecies of Sorghum produced on the near parts of Africa were those that came, as I have shown in the *Kew Bulletin* (p. 116, 1937).

Every new recipient seemed to call it straight away 'millet' or 'grain' in a way that suggests an almost certain traffic in the grain before the raising of the plant; and so it fails to be singled out in the records. Pliny is informative in regard to its coming to Italy: "within these last ten years," he says, writing in the middle of the 1st century A.D., "there has come from India, a millet black in colour, generous of grain, like a reed in stem, reaching 7 feet, and yielding more freely than all that fruits". I believe that this plant, holding on in Italy in an obscure way, became the Mediterranean Broom-corn, of which we pick up traces when the Dark Ages closed.

The Tamarind (*Tamarindus indica*) may or may not have been carried over the Sabaeen lane: this depends on whether it is native in India as well as in Africa; if it is not a native of India then it was carried over. The cereal, *Eleusine coracana*, was carried over; so also the Cotton, *Gossypium herbaceum*, this from East to West (see J. B. Hutchinson & Silow, *Evolution of Gossypium*, p. 83, 1947), and the Banana (*Musa paradisiaca*), to become an exceedingly important food crop in Uganda. Late in time the Sugar-cane (*Saccharum officinarum*) and the aroid *Colocasia esculentum* travelled the same way. Our

information that the Sugar-cane did so, rests on a statement that Dioscorides made towards the end of the 1st century A.D. that sugar was obtained from Arabia Felix ; but the transfer of *Colocasia* cannot be nearly dated. The Bulrush millet (*Pennisetum typhoides*) and the tuberous *Coleus dysentericus* Baker, travelled to India over the lane (for the latter see N. E. Brown in *Kew Bull.*, p. 11, 1894, where the synonym *C. tuberosus* Benth. is used). I have found an unexpected illustration of apparent transfer from Asia to Africa in Vavilov's excellent account (*Bull. appl. Bot.*, 16/2, 1925) of the varieties and races of Flax (*Linum usitatissimum*). Vavilov collects a group of races together under the name 'Microspermae'; they occur through Asia Minor and Persia to Afghanistan, then south through India and reappear in Abyssinia, whither I think they



FIG. 6.—Africa zoned culturally ; the equatorial forests cross-hatched ; the L-shaped area of Sorghum land shaded.

must have been carried from Asia. They are not in Egypt where Flax is in a form spread around the Mediterranean ; and so the intriguing result of Vavilov's taxonomy is another doubt regarding Vavilov's own supposed close relationship of Abyssinia and Egypt. Helena Barulina in her account of the lentils (*Bull. appl. Bot. Suppl.*, 40, 299, 1930) remarks that the lentils of Abyssinia approach the lentils of Afghanistan and India.

I feel that I should mention the Calabash Gourd (*Lagenaria vulgaris*) as a possible illustration of transfer from Africa to Asia over the lane. This interesting gourd is the best of all gourds for calabashes because its surface tissue hardens more than that of any other gourd. The natural wit of Man was bound to use it as a receptacle if he had it to hand ; and he has had it in the New

World as well as in the Old. A question thence arises—by what means did it get either to the Old from the New or to the New from the Old. There are fantastic theories about demanding that unknown voyagers at a strangely early date carried it (and cotton also) across the Pacific. My own belief is that Nature made it common to the Guinea and Brazilian margins of the Atlantic and that it spread thence. Gordon Childe (*The Aryans*, p. 127 of ed. 1, 1926) says that the Aryans had calabashes at 2000 B.C.; and we know that Mediterranean folk in classical times had calabashes made from this gourd as well as from a few others and used them for wine bottles, even considerably, and splashed themselves in the baths with water from them. If the use of calabashes at 2000 B.C. be continuous with use by the Greeks and Romans as is probable, then we need to account for the coming to south-western Asia of *Lagenaria vulgaris* and a natural way would be by the Sabaeen lane.



FIG. 7.—The dispersal of wheat-fields in India.

It has been pointed out by Sir David Prain and me (*Ann. R. Bot. Gard. Calcutta*, 14, 318, 1938) that the African landfall of the Sabaeen lane was inhospitable to such plants as the Greater Yam, being far too dry for its thrift. So too for other plants, whose coming to Africa from the East was delayed until the Yemenite Arabs had so developed their colonies in Zaquebar as to make a home for them. This they did between the 8th and the 11th centuries A.D. The route from Yemen to Zanzibar and also to the Majunga coast of Madagascar is indicated in the map (fig. 6). The L-shaped shaded area in Africa marked on that map, the area where the Sorghums were ennobled, comes to the coast in Zaquebar. Within the two limbs of this L is the humid equatorial forest area with its own cultigens; and the L-shaped area has cultigens of its own likewise. It is to be observed that the forests nearly cut Africa into two; and it is to be added that east of the end of the forest there lies land desert enough to take a part in the cutting, but leaving a channel in the latitude of the Victoria Nyanza. I pointed out in the *Kew Bulletin* (p. 115, 1937) that J. D. Snowden's excellent taxonomic study of the Sorghums (*The cultivated races of Sorghum*,

1936) suggests that the gap serves as a recasting factory between the northern and the southern Sorghums, all the species losing their identity in it. Thus viewed the gap divides the L into two parts. The races of Sorghum which were taken early to Asia were those of the eastern end of the northern limb of the L ; and they had been evolved by selection on it. I take it as important to note how closely their development was hid from the Mediterranean, for we begin to understand by observing such to occur what a real barrier the Sahara was. The way out was sideways by the Sabaean lane. It is recognized that Africa has been comparatively ineffective in plant ennoblement. Vavilov, counting up the cultigens of different parts of the world, stated that no Continent among those that he had studied showed up so badly as Africa (*Origin, Variation, Immunity, Breeding cult. Pl.*, p. 14, 1951). However, on the northern limb of the L some curious ennoblements have been accomplished. There we find as a pulse the geocarpous Leguminosa, *Kerstingiella geocarpa*, and a source of oil one of the



FIG. 8.—The dispersal of rice-fields in India.

Polygalaceae, *Polygala butyracea*, and a small millet, *Digitaria exilis* Stapf. (I reduce *D. iburua* Stapf). The angle of the L appears likely to have seen the ennoblement of *Coleus dysentericus* Baker, and *C. dazo* A. Chev. & Perrot, at least in part.

The cross-hatched area in the map is a country of yams, comparable therefore, with the humid forests of the Malay Peninsula where the Semang live ; but less striking in results. The chief Dioscorea of the Guinea forests, *D. cayenensis*, when brought by the Portuguese into competition with the Asiatic *D. alata*, took second place. The Guinea palm which supplies oil (*Elaeis guineensis*) is not the equal of the eastern Coconut palm ; and the leading masticatory nut, the Cola nut, though enormously prized by habitués, has not excited the cultivation that the Areca nut has.

Because drier climates so effectively hem in this humid area, its ennobled plants were retained within it until shipping carried them across the Atlantic.

I proceed to India and commence with fig. 7 giving the dispersal of wheat-fields in India which simulates a scattering before a north-west wind, and fig. 8 of the dispersal of rice-fields in India which suggests a flooding from the East. The two maps should be compared. They represent what has happened, namely a borrowing of the one cereal from the West and of the other from the East. Then follows fig. 9 which gives the dispersal of Sorghum in India. This is grown in the season of Rice where Rice cannot be readily grown, and it demands less water than Wheat and therefore is grown, where to raise Wheat is difficult. The actual intensity of Wheat and Rice has been greatly altered by the irrigation engineer ; but the antithesis of Wheat and Rice remains and powerfully affects the dietaries ; for instance, a high-caste man can be a complete vegetarian on Wheat and pulses, but with difficulty on Rice without fish ; therefore there are Brahmins who eat fish lest their race perish.

There is another West versus East contrast that is peculiarly interesting ; it is in the sources of oil. From the direction of the Pacific at a remote time came the Coconut palm (*Cocos nucifera*) finding the humidity necessary for its



FIG. 9.—The dispersal of Sorghum in India.

thrift easily so long as it grew near the sea and using as means of transport for its large fruits the ocean currents. It may have reached India naturally, if also with Man's help. It has been proved by Man's planting that it can be grown in the interior of Bengal even at 200 miles inland, but could not have got there without Man ; on the Bombay side there is one place where it has been grown at 80 miles from the sea ; but north of the Arabian Sea it will not grow—not even by the sea. Therefore there was a time when the Sind coast and the greater part of the interior of India were without the pleasant oil that it gives. The areas there without easy supplies now grow Sesame, Hemp, Linseed, the Castor-oil plant, Poppy and certain Brassicas, and again, not to misrepresent the case, the Niger seed plant (*Guizotia abyssinica*) which has not had a long history in India, and towards the north-east *Perilla ocimoides* which has come

round the corner of the Himalayas from the direction of China. * Paying attention to the first six, it is noticed that all of them are plants that have come from the West. When? I believe from the time of the Indus civilization, which is dated as around 3250-2750 B.C. The implication on observing the sources of oil to have come from the West, the known fact that there was a connection between the Indus and the Sumerian civilizations, the presumption that the founders of the Indus civilization were intruders into an India of Dravidians, is that India had been dependent on such forest trees as *Schleichera trijuga* Willd. for its oil, except where the Coconut was available, until the Indus civilization was introduced.

I have laid out my observations in a way which permits me to suggest that the triangle which I have defined as India was the meeting ground of two spreading cultures, the one dominated by the history that I have been tracing, the other something which originated in Indo-China beyond the reach of the domination. Unfortunately it is very difficult to envisage the beginnings of this new culture. Indo-China is more the land of the bamboo than any other part of the world; with the aid of the bamboo the building of a new house is delightfully easy, and kings would think nothing of compelling the complete removal of a capital. The face of the land changed as migrations blotted out the old physiographic characters. But if the Mon came into Indo-China about 2000 B.C. they must have had a large part of shaping the culture.

Clay tablets exist showing shipping in the Persian Gulf in the days of Ur. Mohenjo Daro was not too far from the coast to benefit by an extension to it; but Harappa was by the river Ravi, far inland; and it was in Harappa that Sesame seed was found. Presumably, therefore, Sesame was cultivated through the Indus civilization and possibly the agriculture of Sumeria had taken hold of a fairly large part of northern India. We do not as yet know the language used then. When the Aryans had taken the Punjab they left records in vedic which one dates as of 1000 B.C. and the immediately following centuries; then the language changed to pali and from pali it became sanskrit, which in turn began to break up into the current Indian Indo-Aryan vernaculars about A.D. 800, but lingered, like monkish Latin, to later than A.D. 1500. It used to be customary in botanical writings to welcome a sanskrit name as a sign of ancient cultivation; it is obvious now that we have deeper sources and some reason for using the evidence of sanskrit names with care. Sanskrit is not older than Latin; vedic is. A name for Sesame appears in vedic—tila, passes through sanskrit and persists today. The seed, we know, was eaten as a porridge with pulse or cereal grain; and as a source of oil its importance was so great that its name meant oil, the metonymy being from oil to Sesame; and in that case all the other oil seeds raised would be secondary to Sesame at the time when Sesame obtained its name among the Aryans.

There is evidence that the Aryans came into India using hempen ropes, with 'bhanga' as a name for Cannabis fibre. They may have been users of hemp-seed oil before they contacted sesame oil and found it better.

There is a vedic name, 'erand', for the Castor-oil plant which likewise passed through sanskrit to the modern Indo-Aryan vernaculars. It invaded Chinese as 'i-lan' and exists in the Dravidian language, pushtu, as 'arhand'. Kittel has suggested that this name was originally Dravidian and borrowed by the Aryans, which supposition accepts the Castor-oil plant as in India before the Aryans came. A great abundance of additional names in sanskrit attests to great familiarity with it; it was 'chatravija' or painted seeds, 'pancanguri' or five-fingered leaves, etc., as well as 'erand' and 'amanda'; and 'amanda' links up with 'amadam' in telegu and 'amanakkam' in tamil. Kittel's supposition seems good; and the conclusion can be sustained that the Castor-oil plant was spread through India before the Aryans came. It would be a basic oil plant for illumination and for anointing the body as it had been earlier in Mesopotamia (see Campbell Thompson, *op. cit.*, p. 130).

There is a third oil-seed with a vedic name, 'sarshapa', a Brassica; but no vedic name has been detected for Linseed and Poppy. Yet Linseed has a name in pali and poppy in sanskrit. Surely the absence of a name for Linseed in vedic does not prove its absence; but it is easy to believe that the Poppy came late.

I have used Duthie and Fuller's *Field and Garden crops of the United Provinces* as a guide to furnish an authoritative list of what justifiably can be called the current important crops of the Upper Gangetic plains; and I have analysed my list, extracting out of it in the first place the crops that are sown in October. They are Wheat, Barley, Safflower, Opium poppy (grown for oil), Lentil, Field pea, *Lathyrus sativus*, Linseed and three Brassicas. They are all crop-plants of south-western Asia and the quantity of all of them that is grown decreases eastwards towards Bengal where they almost if not entirely disappear. It is obvious that they are crops brought to India from the West, requiring the 'Cold weather' for growth, strangers originally. Then I extracted from the work the crops sown in May. They are the grain crops, *Setaria italica*, *Paspalum scrobiculatum* and *Eleusine coracana*; and the pulses *Phaseolus aureus* Roxb. (including *P. radiatus*), *P. mungo* L., *P. calcaratus* Roxb. and *P. aconitifolius* Jacq. They ripen in three months; and nothing that requires more time can be used, for the crop must be harvested to make way for the October sowings. They are of various origins, but the pulses are endemic to India; the first named being a very valuable plant. Prain suggested (*Journ. As. Soc. Bengal*, 66/2, p. 433, 1897) that the wild *Phaseolus sublobatus* Wall., a weed of field margins and like places from the Bombay coast to the China Sea and to the Philippines, gave rise to it as well as to *P. mungo*, which is reasonable; but it may be that *P. aureus* had multiple origins, not all of them within India. That the other Phaseoli had their origination in India is incontestible. Over and on the eastern limits of India, *P. ricciardianus* Ten. takes a place in cultivation and in central China *P. chrysanthus* Savi. *P. aureus* has a vedic name. In India but not quite to the very north, *Panicum miliare* enters this group of crops and, to a small extent, *P. psilopodium*, which is believed to be parent of *P. miliare*. A cultivation of parent and extraction in the same country shows that state which I have called semi-ennoblement, a state in which ennoblement is always liable to be frustrated by want of isolation. To the list of leguminous crops that India originated may be added *Dolichos lablab*, but ennobled for greens. India accepted two other Leguminosae, *Cajanus indicus* and *Vigna catieng*. India ennobled a series of Cucurbits, also for use as greens, being such as do not have fruits too heavy for suspension—*Momordica charantia*, *Trichosanthes dioica*, *T. cucumerina* and *Coccinia indica*. But all of these except the *Momordica* are only semi-ennobled, fruits of wild plants being brought to the table as sufficient without the ennobling. *Trichosanthes anguina* is completely ennobled, with *T. cucumerina* for parent.

The Egg-plant (*Solanum melongena*) seems to stand as a cultigen entirely to the credit of India. Like the Cucurbits, it serves as greens, the fruit being cooked at a slightly immature stage. Its origin has been much disputed, but I believe that taxonomists will find within var. *insanum* a parental form. Originally the plant was round-fruited and would carry several fruits together. Selection was directed to getting a larger fruit and that became associated with fruits tending to be solitary. As a round fruit, the sanskrit name 'varta' or 'vartaka' was appropriate, for the word is traced to an adjective meaning round. As round-fruited it reached China; and so it happened that a Chinese visiting Samarcand in A.D. 1221 expressed his surprise at finding there the fruit elongated (Bretschneider, *Mediaeval Res.*, 1, 89, 1910). The plant must have reached Malaysia with relatively small round fruits; otherwise the Malays would not have classified it as a 'têrong' along with their several species of *Solanum*. 'Varta' gave rise to 'baigun' in India, 'bedingan' in the Levant, then when the Arabs took it to Spain 'berenjena', and with the definite article prefixed 'albergine' in french—an interesting sequence which embodies much history. Ennoblement

seems not to have been very remote in time, but rapid enough for different countries to contain new forms differing in a degree that enabled Filov to group them geographically (*C.R. Acad. Moscow*, **26**, 815, 1940).

Alocasia indica is another plant ennobled in India for service as greens ; but it became overshadowed when *Colocasia esculentum* was brought from the eastward. India would be greatly led towards ennobling greens because they were wanted for service with the Rice.

India originated the cultivation of the Mango (*Mangifera indica*) and the Jack-fruit (*Artocarpus integra* Merr. or *A. heterophylla* Lamk.), some other species of *Artocarpus* and various species of the genus *Citrus*, and borrowed from Indo-China many plants for additional ennobling. There is no cleavage between botanists in regard to the part of the world within which Rice originated, but much uncertainty in regard to the manner in which it originated within that part. Dr. D. Chatterjee's " Note on the origin and distribution of wild and cultivated Rices " (*Ind. Journ. Genetics and Pl. breeding*, **11**, 18, 1951) supplies a good starting point for understanding the position. Rice undoubtedly came into cultivation in Indo-China. It is just possible that the area extended into adjoining India. Thence it spread across India, apparently taking wild rice with it, for it is difficult to believe that the wild rice, now accompanying it, was there before. The vedic Aryans knew Rice. It does not happen to be mentioned in their oldest book, but that does not prove its absence. Continuing to diffuse westwards from India it was in Mesopotamia in the 7th century B.C. (Campbell Thompson, *op. cit.*, p. 105)—a slow but not unusually slow progression. As it crossed India Wheat would so to speak fight back and delay it ; and still more so after the boundaries of India had been crossed.

The Greater Yam (*Dioscorea alata*) came into India out of Indo-China. In its case we are able unusually narrowly to indicate where its cultivation originated ; it was just beyond the Cupuliferous boundary line. I summarized its history in *The Advancement of Science* (**7**, 443, 1951) and do not need to add anything here.

A home of *Musa balbisiana*, parent of the Banana, is where the Greater Yam originated. Cheeseman (*Kew Bull.*, p. 148, 1948) recommends that *Musa paradisiaca* L. be accepted as a name for the cultivated Banana, with *M. balbisiana* Colla as a name for the wild parent. But *M. acuminata* Colla is part-parent of some races of the cultivated Banana. This species also comes from beyond India. The Sugar cane must have entered India by diffusion through Indo-China, for it appears to have originated further east. The chief components of the Betel quid came perhaps by the same way ; but it is probable that the idea of the quid preceded them and that they were betterments. It is recorded of the Betel nut that the Chinese emperor, Wu-ti, after he had annexed the state of Nan-yue (the coastal extreme south of modern China) in 111 B.C., insisted on its cultivation at his palace in Shen-si, along with various oranges, the litchi and the lungnan ; and, says Laufer (*Sino-iranica*, p. 262, 1919), many gardeners lost their lives for failing. The betel palm grows in Hai-nan and had probably reached that island by the time of Wu-ti.

Southwards the region of Indo-China passes into Malaysia, which is the greatest humid region of the Old World. It is apparent that Malaysia was so to speak bombarded from the coasts of Indo-China with migrants who are best called pre-proto-Malays. The date according to some was about 1000 B.C. ; others would have it earlier. Blagden postulated a fringe of these folk on the whole coast from the Irrawaddy to Tong-king (*Journ. R. As. Soc. Straits br.*, **37**, 1902) which looks probable and would account for radiating invasions of the islands such as certainly took place. As coastal, they lived undoubtedly in fishing villages ; and what they took into the islands was the habit of living on fish with such additions as they could get from the land. Kern suggested that they invaded the islands in the possession of the working of iron, the control of the domestic

buffalo and a knowledge of how to grow irrigated rice. The idea that they had iron is now discounted and I think that we must abandon the supposition that they cultivated Rice with the aid of irrigation, but admitting that they had what is called dry land rice. It is quite certain that when they reached Java they came up against a considerable neolithic population. It is well demonstrated that metals came to the islands after these migrants; van Stein Callenfels suggests (*Bull. Raffles Mus. Singapore*, **13/1**, 150) that metals came about 300 B.C. Obviously before this, a migration eastwards had been started that after centuries reached the longitude of Samoa and then fanned out as Polynesians. These kept no tradition of Rice, and worked no iron. In the last centuries B.C. India discovered how to cross the Bay of Bengal and began to make trading voyages to what was called Suvanabhumi or the coast of gold, where lived people who clothed themselves in bark cloth and were ready to buy Indian cottons. There is a story in pali of a voyager who was nicknamed the bark cloth wearer, for, after the misfortune of shipwreck, he clad himself in what he could get; and another of a merchant who by marrying a naked princess got a kingdom. One venture led to another and ultimately to the establishment of powerful hinduized kingdoms in several parts of western Malaysia. These kingdoms brought the land forward greatly and there came about a marked contrast between western Malaysia where they were and eastern where they were not. The West grew rich in rice and the East kept poor. This contrast in the first degree depended on the climate, for large parts of the East are unsuited, and those who live there turn to sago, yams and other roots for starchy food; but the sinews of the western states were certainly in their rice-fields.

This differentiation did not arise immediately; Coedes dates it as "from intense colonization in the 2nd and 3rd centuries A.D. bearing fruit in the 4th and 5th" (*Hist. du Monde, Les états hindouisés d'Indochine et de l'Indonésie*, p. 40, 1948). Towards A.D. 600 the states in Malaysia began to shake themselves free of the influences from India. This having been the history, when we discover an economic plant to have names in Polynesia and Malaysia that show a common origin, we detect pre-hinduization cultivation: when we observe a name in Malaysia to be sanscritic we suspect introduction from India at some date before A.D. 600 and probably A.D. 200-300. For instance, we find the Malay word for yam 'ubi' to be used throughout the Pacific in one form or another, and deduce that Dioscoreas, chiefly *D. alata*, were a very important food at the date of the Polynesians' departure. We find the Malay word 'tēbu' for sugar-cane, 'tales' for *Colocasia esculentum*, 'biah' for *Tacca pinnatifidā*, 'nyior' for Coconut to be repeated, and recognize that the names having travelled with the migrants, the plants had made a large cultivated element in the foods of the pre-proto-Malays out of whom the Polynesians sprang.

The sanscritic vernacular plant names that I have on record are met with in the following languages in this order, Malay, Javanese, Sundanese and then in small numbers further afield on old shipping routes that the Malays used. Only a few refer to foods of importance, the Onion being one of these, the Water melon (*Citrullus colocynthis*) another. Sesame presents a third case, but invites further investigation. It has two widely spread names which appear in Malay as 'bijan' and 'lenga'. The first I believe is from the sanskrit word 'biji', a seed. Why call it seed?—the priests settled that, for it gave the sacrificial oil-seed. They had not needed it in the kitchen with the coconut to hand. 'Lenga' needs tracing. The immigrants were responsible for bringing in improved fruit-trees. The words most usual in Malaysia for the *Citrus* and *Eugenia* fruits are sanscritic and bear testimony to ennoblement in India within the genus *Citrus* and of *Eugenia jambolana*. Ennobled races of *Zizyphus jujuba* must have been brought. The Jack-fruit tree has two names; it is 'nangka' very widely and the origin of that name awaits explanation;

but it has the sanskrit name 'panasa' used as panas, pinasa, lamasa, benaso, etc. in various Malaysian languages, and it is peculiar that 'nangka' had not sufficed where they are. The tree was taken to China under the sanskrit name 'panasa' (altered to po-no-sa) during the short period A.D. 502-557. Chau Ju-kua, Inspector of maritime Trade at Canton in c. 1225, recorded that his countrymen, understanding that it had come from the country of Po-lo, suspected a mistake and renamed it po-lo-mi; and as such or as po-lo-mat and po-lo-mit it has remained save that truncated to mit (cay mit or tree mit) it has entered anamese. Hirth and Rockhill suggested Fu-nan to be Po-lo and that was certainly right; the tree was passed forward to Canton from that hinduized kingdom (Hirth & Rockhill, *Chau Ju-kua*, p. 212, 1911). *Cajanus indicus* and Cucurbits of the genera *Luffa* and *Trichosanthes* have sanskrit names and may be adjudged introduced cultigens. But the majority of the sanskrit names do not indicate supplies for the kitchen so much as royal pomp or priestly observances. The rulers laid out parks after the Indian manner, planting what the ruler of one state called in 775 A.D. 'lordly trees' (see *Proc. Linn. Soc.*, sess. 156, p. 88, 1944), such as these, *Michelia champaca*, *Mimusops elengi*, both natives of India brought for their scent, *Cassia fistula*, *Elaeocarpus ganitrus*, *Anthocephalus cadamba*, *Mesua ferrea*, *Albizia lebbek*, *Schima noronhae* and *Calophyllum inophyllum*, trees which might be found with trouble in Malaysia but with ease in India. The priests according to their observances, whether brahmin or buddhist, needed *Ficus religiosa* but *F. rumphii* was acceptable as sufficiently similar; needed *Saraca indica* but would accept *Ixora coccinea*; needed the Sacred lotus and multiplied the tanks in which it was grown; the worshippers of Shiv required his emblem of trifoliate leaves which they obtained in *Aegle marmelos* or *Feronia limonum* or *Butea monosperma*. Of these *Ficus rumphii*, the *Feronia* and the *Butea* were available in parts of Malaysia; the others were brought as cultivated plants from India. The Malaysian *Ficus septica* was accepted for the Indian *F. glomerata*. *Calotropis gigantea* has a sanskrit name and religious use for which it was grown. As pleasant *Ocimum* was raised; for dyeing *Woodfordia floribunda* and *Carthamus tinctorius*, the latter certainly, the former probably brought from India. The Castor oil plant was introduced. *Moringa oleifera* was brought in as a condiment. The two peppers, *Piper nigrum* and *P. longum* were brought also. A love of intense scents led to the bringing of *Hedychium coronarium*, *Hibiscus abelmoschus* and jasmynes. I have not mentioned the Mango (*Mangifera indica*) because its names are not actually sanskrit; mempalam is from one Dravidian language and mangga from another; but it had come from India. Nor have I mentioned *Paspalum scrobiculatum* because its name in Java, 'kodoan', is likely to have come from Gujarat in A.D. 611 with the fugitives whose arrival is depicted on the Borobudur temple. 'Jelita' for *Corchorus capsularis* in eastern Malaysia possibly came by slaves brought from Chittagong by the Dutch.

I have sought for a return from Malaysia to India and find only two plants, neither beyond doubt. One is the Sandalwood tree (*Santalum album*). Fischer (*Kew Bull.*, p. 200, 1927 and *Journ. Bombay Nat. Hist. Soc.*, 11, 458, 1938) pointed out its discontinuous distribution in India and indications that it is spreading as evidence of having being introduced. The only contribution that I can make is to call attention to the double evidence of its arrival in Ahmednagar towards the reign of Akbar (A.D. 1560-1605). Abu'l Fazl states in his 'Ain-i-Akbari' that it had been brought but does not precisely date its arrival. Garcia da Orta whose Colloquies were published in 1561, states that he had seen the tree at Ahmednagar; and it happened that Akbar besieged Ahmednagar in 1560. It is clear that it was a novelty at the town which is 120 miles due east of Bombay city and must have been brought thither from southern India a little before 1560. The other possible introduction from

Malaysia is the patchouli, *Pogostemon heyneanus* Benth., brought first in an inferior race, then in ennoblements.

After the sanskritic influence had gone, Malaysia obtained a knowledge of many plants from the Arabs and Persians who came trading by ship with dry goods and lodged a few economic plants. At the same time and indeed earlier the Chinese were bringing their own plants to Malaysia, and by their names we know that they introduced *Acorus calamus*, *Aglaia odorata*, Chinese chives (*Allium odorum*), Celery (*Apium graveolens*), Wormwood (*Artemisia vulgaris*), the Tea tree (*Camellia sinensis*), *Chrysanthemum coronarium*, *Lycium chinense* and the Litchi (*Litchi chinense*). Because the Chinese language is uncouth to Malay ears, there could have been an unwillingness to adopt names of various additional plants.

Carrying on with the help of Indo-Chinese, Indian, Persian and Chinese loans, Malaysia has done very little origination and ennobling of cultigens. A few years ago I was able to obtain from two friendly Malays of different villages near Telok Anson, Perak, lists of the substances that they ate with the daily rice, by name and by weight. A Malay likes two substantial meals a day and each consists of rice and of something eaten with the rice. My useful friends, under the direction of Mr. E. F. Allen of the Department of Agriculture, Malaya (to whom I am exceedingly grateful), kept up their returns from November 1946 to March 1948, during which time they resorted to over 100 different food-plants, I have analysed the returns grouping the vegetables under (a) native plants such as a new Malay settlement might fall in with, seek, and use; (b) Indo-Chinese plants, such as the pre-proto-Malays would be expected to know; (c) Indian and Chinese loan plants; (d) loan plants that came from further away through India or China and (e) American plants not available until after A.D. 1500. By weight converted to percentages, my friends used: (a) 16; (b) 30; (c) 23; (d) 12 and (e) 18. It is interesting that even the American element came to table in greater quantity than the native. Colonization without support is difficult in proportion to the land's lack of resources and it is obvious that the first comings of the pre-proto-Malays, as the comings were not massive, must have been far too difficult for the bringing of Rice irrigation. Irrigation came with the state-building activities of the Indian adventurers; and their settlement in western Malaysia and absence from eastern Malaysia were a major factor in creating the difference of which I have written. I would add that as showing the need of state-craft for irrigation: the Malay Peninsula continued to grow little but dry-land rice until British administration, about eighty years ago, created a secure land tenure that enabled irrigation to be undertaken.

The reader may be interested in knowing what were the most used components of the meal with the rice—in greatest quantity the terminal parts of banana inflorescences, something comparable to a cauliflower, consisting of male and sterile flowers; then (2) fruits of the Egg plant (*Solanum melongena*) slightly immature; (3) cucumbers; (4) tubers and petioles of *Colocasia esculentum*; (5) fresh new leaves of the uncultivated fern *Diplazium esculentum*; (6) fruits of *Musa* in immature stages; (7) shoots and young fruits of the Jack-fruit tree; (8) pineapples; (9) *Ipomoea reptans*, partly from wild sources and partly from Chinese cultivation; (10) legumes of *Vigna sinensis*; (11) tubers of the Sweet potatoe (*Ipomoea batatas*); (12) seedlings of *Vigna sinensis*, 3-4 days old, as prepared by the Chinese; and so forward. I intend to publish the full data in *The Gardens Bulletin, Singapore*, and will not burden this paper with more.

It seems clear that the pre-proto-Malays came with dry-land rice and the tubers that the Polynesians relied on, the Greater yam and *Colocasia*, the tubers of *Tacca pinnatifida* and probably the cereal Job's tears (*Coix lachrym-jobi*) and some ennobled Musas and kept up the ennobling of these while reliant

on their fishing and what the uncultivated land provided, the resources of the cultivations to the west being unknown.

When we have dated the coming of the pre-proto-Malays as 1000 B.C. and the beginning of tillage in Inner Asia as perhaps 7000 B.C., the lateness of Malaysia is impressive and then the smallness of achievement towards ennoblement is understood. It seems reasonable to surmise that beginnings in China and India might have been before 4000 B.C. and beginnings at the southern end of the Red Sea a little earlier; but in Africa at large very much later.

Man has taken an enormous time everywhere in effecting very little. The pattern has been cereals first if available, then pulses if available, then greens and roots, etc.; and the more humid parts of the world have been such that Man had to start without the advantage of cereals and pulses and with the disadvantage of the materials being perennial. Perennials are most intractable if they be tall trees with cross-pollinated flowers fertilized by uncontrolled pollen. Even the Durian (*Durio zibethinus*) has had very little ennoblement; the Jiring (*Pithecellobium jiringa* Prain) very little; the Rambutan (*Nephelium lappaceum*) none. On the other hand, the Bread-fruit (*Artocarpus communis*) has had much in the Pacific islands, where the isolation of the islands has contributed and every tree has been under observation. In the ennobling of Yams and Colocasia the Polynesians took a pride; it was a mark of distinction to possess a clone or race that a neighbour did not know; but such emulation is now passing away.

After A.D. 1500 American plants were spread with very great rapidity, particularly those that made a quick return such as Maize. But with them I cannot deal.

The PRESIDENT expressed the thanks of the Meeting to Mr. Burkill for his Lecture.

PRESIDENT'S RECEPTION

Thursday, 6 December 1951, at 8.30 p.m.

The PRESIDENT, Professor F. E. FRITSCH, F.R.S., received the Guests in the Library.

Dr. C. F. A. PANTIN, F.R.S., showed a film illustrating the behaviour of the sea-anemone, *Metridium senile*. The film was prepared at his suggestion by Dr. E. J. Batham and Mr. P. M. B. Walker. It is a quick-motion film in which one minute of film time corresponds to one hour of real time. It shows firstly that these apparently inactive animals have in fact a very complex behaviour, which is too slow for us normally to appreciate; secondly, that much of this behaviour appears to be spontaneous and does not consist of simple direct responses; thirdly, that it is highly purposive. Dr. Pantin briefly discussed the influence of these observations on our conception of the behaviour of the lower animals.

EXHIBITS IN THE LIBRARY.

THE INSTITUTE OF SEAWEED RESEARCH, INVERESK. The work of the Institute.
[Shown by Mr. F. T. WALKER.]

(The programme of research of the Institute covers a wide field ranging from surveys of the algae growing around the coasts of Scotland to the utilization of seaweeds, their constituents and derivatives.)

Much of the fundamental work is extra-mural, being carried out at universities and colleges such as, methods of chemical analyses (Edinburgh

University), presence of trace elements (Macaulay Institute), iodine compounds (Leeds University), types of proteins (Oxford University), poultry feeding (Reading University), pig feeding (Agricultural Colleges), fertilizers (Nottingham University). The Universities of Glasgow, London, Cambridge and Durham are also participating.

The exhibit was therefore of necessity very restricted and comprised the following items: a mosaic of aerial photographs by Coastal Command, Royal Air Force, by whom the Institute is assisted in its preliminary sublittoral surveys of the sea bed; a photograph showing quadrat sampling of the sea bed from a motor vessel by which method detailed surveys are carried out; samples of the chemical constituents of *Laminaria cloustoni*, chief of which are alginic acid, mannitol, fucoidin, laminarin (experiments are in hand using the last named as an addition to the blood bank).

The products of industry were represented by cones of continuous fibres of calcium alginate extracted by Alginate Industries, Ltd. and spun by Courtauld Ltd. This fibre is soluble in mild alkali and is incorporated in the fabrication of superfine woollen materials where the alginate yarn is used for strengthening the woollen yarn later to be dissolved out. A sample woollen fabric by Silkella Ltd. was exhibited.

Calcium alginate fibres, made up into bandages and swabs for internal surgical uses by Medical Alginates Ltd., were also exhibited. These tissues are haemostatic and become absorbed as the wound heals.)

BRITISH MUSEUM (NATURAL HISTORY). Long-horned Timber Beetles (Cerambycidae). [Shown by Mr. J. BALFOUR-BROWNE and Mr. E. A. J. DUFFY.]

(During the last few years the importation of increased quantities of both hardwoods and softwoods from many unusual sources has led to the introduction of upwards of 100 species of Cerambycidae, the majority of which were represented in this exhibit.

As a rule these insects are imported in the larval stage and the adult beetles may not, in some cases, emerge for many years. As an example of larval longevity a living larva was exhibited which was known to be over 25 years old.

There is good reason to suppose that at least a few species previously unknown in Britain have now become established in this country as a result of recent importations of timber from the Black Forest of Germany. As a general rule most tropical species fail to attain maturity unless they were already in the pupal condition at the time of arrival.

The immature stages of certain species and a small selection of damaged woods were exhibited, also a series of drawings to display the diversity of structure in the larvae and pupae of this large and economically important family of beetles.)

BOTANICAL DEPARTMENT, BIRKBECK COLLEGE. Structurally preserved Abietaceous Cones of Wealden Age. [Shown by Mr. K. L. ALVIN.]

(The exhibit was designed to present the outlines of the technique employed in studying the structure of lignitic (non-petrified) cones from the Wealden clays of the Hainaut district of Belgium, and to show the main features of interest in the species.

The material, a sample of which was available for examination, is of a hard coaly nature, but can be softened by treatment in alcoholic potassium hydroxide, embedded in celloidin, and sectioned on a 'sledge' type microtome.

The technique is not a new one, but is open to considerable modification according to the condition of the lignite.

Specimens of three species were exhibited together with photomicrographs showing their internal structure. All three species, although differing appreciably in both external and internal form, fall naturally into the Abietaceae, and have been provisionally placed in Nathorst's form-genus *Pityostrobus*. One species, *P. andraei* (Coemans), appears to be closely related to recent 'hard' pines; another, a new species, seems closer to the 'soft' pines. The third, *P. corneti* (Coemans), although resembling a cone of *Cedrus* or *Abies*, presents a combination of anatomical characters more in keeping with those of *Keteleeria*.

The material belongs to the Natural History Museum, Brussels, and forms part of the Bommer Collection. A detailed description will later be published in the *Mem. Mus. Roy. Hist. Nat. Belg.*

ZOOLOGICAL SOCIETY OF LONDON. Some terrestrial Arthropoda. [Shown by Mr. L. C. BUSHBY.]

FOREST PRODUCTS RESEARCH LABORATORY, PRINCES RISBOROUGH. Wood-rotting Fungi. [Shown by Dr. W. P. K. FINDLAY.]

(The following exhibits were shown by Mycology Section of Forest Products Research Laboratory.

1. Cultures of wood-rotting fungi fructifying on malt agar.

As an example of their use in recognition of the cause of decay in samples of decayed wood sent in for diagnosis, a culture *Ganoderma collossus* isolated from heart rot in *Cassia siamea* was shown.

The odours produced by wood fungi in culture are often characteristic and enable them to be recognized. Some of the sweet smelling volatile products metabolized in culture by lignicolous fungi have been isolated and identified chemically.

2. Coloured transparencies of fructifications of the dry rot fungus, *Merulius lacrymans*, taken on Ektachrome film.
3. Sections, photomicrographs and specimens of wood attacked by Ascomycetes such as *Chaetomium*.

The hyphae of these fungi penetrate the cell walls of the wood longitudinally, often eroding prismatic cavities therein, in contrast to ordinary wood-rotting Basidiomycetes which penetrate cell walls transversely.)

Dr. C. F. A. PANTIN, F.R.S. Preparations of the nerve-network in Actinians.

(Microscopical preparations were shown illustrating the muscle system and the nervous system of the sea-anemone, *Metridium senile*. There were shown :

1. An Heidenhain preparation showing the network of muscle fibres in the general muscle field.
2. Silver stained preparations (Batham's modification of Holmes's method) showing the network of bipolar nerve cells and the structure of the synaptic contacts between them.)

ROYAL BOTANIC GARDENS, KEW. The Genus *Sphaeranthus*. [Shown by Miss STELLA ROSS-CRAIG.]

(The Genus *Sphaeranthus*, which is now under revision, is a genus of the Compositae comprising about thirty-eight species. The exhibit demonstrated that the flowering heads are made up of a number of capitula borne on a common receptacle: each capitulum consists of a number of female flowers, a lesser number of male or hermaphrodite flowers and a varying number of bracts, with an outermost or subtending bract. The division of the genus

into five main groups, on the basis of receptacle, capitulum and bract characters was shown. The groups were :—

1. Receptacle globose or elongated, capitula fully exposed, subtending bracts hidden, or almost hidden.
2. Receptacle globose or subglobose, capitula more or less hidden, subtending bracts conspicuous, at least at the base.
3. Receptacle flat or almost flat capitula exposed, subtending bracts hidden.
4. Receptacle flat, capitula almost hidden, subtending bracts conspicuous.
5. Receptacle elongated or rarely oval, capitula more or less completely hidden, subtending bracts very conspicuous, overlapping and forming a conifer-like cone.

The exhibit also showed the distribution of the genus, which, except for a small area in Iran and Persia, is confined to the tropical and sub-tropical areas of the Old World.)

ROYAL NAVAL SCIENTIFIC SERVICE. Some biological aspects of ship fouling. [Shown by Mr. N. INGRAM HENDEY and Dr. H. G. STUBBINGS.]

(The exhibit showed the main fouling organisms which occur on the hulls of ships operating in British waters, arranged in order of decreasing sensitivity to cuprous oxide, the more commonly used poison contained in anti-fouling paint. The groups included biological slime (chiefly diatoms and bacteria), *Tubularia* sp., *Balanus* sp., *Ectocarpus* sp., *Tunicata*, *Porifera*, etc.)

Items of special interest were specimen test-panels from Home Waters and the Persian Gulf showing attached fouling, and a model section of a ship's firemain fouled by *Mytilus edulis* Linn. Photographs depicted an Admiralty raft for the immersion of test-panels, comparative examples of effective and ineffective anti-fouling paints, fouling *in situ* in ships' fire-mains and the immigrant Australian barnacle, *Elminius modestus* Darwin, now abundant around our coasts. Others showed a selection of the diatoms which formed the major part of a biological slime on non-toxic panels from the Persian Gulf, immersed for studies on fouling intensities.)

ROYAL HORTICULTURAL SOCIETY. Original coloured drawings of Chinese plants made at Canton and Macao in the early nineteenth century for the Horticultural Society of London under the supervision of John Reeves. [Shown by Mr. W. T. STEARN.]

(In the early 19th century, when little was known about the Chinese flora, the Horticultural Society of London requested John Reeves (1774-1856), an East India Company's tea inspector at Macao and Canton, to procure coloured drawings of ornamental Chinese plants from which the Society could ascertain those worthy of introduction to British gardens. Several hundred illustrations were accordingly painted by Chinese artists under Reeves's supervision. One of them received in 1819 led to the introduction of *Primula sinensis*. Lindley described two new species, *Bulbophyllum bicolor* Lindley, *Gen. Sp. Orchid*, 49 (1830) and *Cymbidium floribundum* Lindley, *Gen. Sp. Orchid*, 162 (1833) from these "ic. pict. Sinens. in Bibl. Hort. Soc.". Historically as well as artistically they are of high value. Financial difficulties caused the Society to sell them in 1859 and all trace of them was lost until 1936 when they came into the Lindley Library of The Royal Horticultural Society as a bequest from Reginald Cory, who had known nothing of their history. Their identity with the long lost Reeves drawings was established by the Society's Librarian, Mr. W. T. Stearn; an account will be found in E. H. M. Cox, *Plant Hunting in China*, 52-57 (1945). The illustrations shown portrayed

Cymbidium floribundum Lindley, *Primula sinensis* Lindley and *Strophanthus divaricatus* (Lour.) Hooker & Arn.)

BRITISH MUSEUM (NATURAL HISTORY). Past climatic changes as revealed by deep-sea cores. [Shown by Dr. J. D. H. WISEMAN and Mr. C. D. OVEY.]

Mrs. VERA HIGGINS, V.M.H. Examples from the genus *Euphorbia* to show the range of form amongst the succulent types.

(The exhibit consisted of succulent *Euphorbias* arranged to show the types predominating in the areas where they occur. The American spineless types with reduced leaves were represented by *E. antisiphylitica*, *E. missouriensis* and *E. pteroneura*; from the Canary Isles, *E. balsamifera* exemplified the species with swollen stems and leaves only at the tips of the branches, whilst the spiny types were represented by *E. canariensis* and the rare *E. handiensis* found only on Fuerteventura. In North Africa species with angled, spiny stems predominate, e.g. *E. baumieriana* and *E. resinifera*, but in South Africa the succulent species attain their highest development; *E. pseudocactus* and *E. squarrosa* illustrated the species whose pairs of spines along the angled stems are derived from stipules, *E. horrida* those whose spines are derived from short lateral shoots which abort and become lignified and *E. valida* those where the peduncles become lignified after flowering. There are also spineless types with round stems, e.g. *E. mauritanica* and *E. Dregeana*, while *E. caput-Medusae* and *E. gorgonis* represented the species which have short lateral branches arising from a central 'head'. In Madagascar the most common form has rounded stems with scattered spines and an annual development of leaves, e.g. *E. splendens* and *E. Hislopii*, and the Indian species *E. nerifolia* and *E. nivulia* indicated the types found there, with succulent stems, few spines and leaves developed annually. Amongst the 50 species shown were a number rarely seen in cultivation in this country such as *EE. hamata*, *aspericaulis*, *deceptor*, *silenifolia* and *restituta*. The plants were from the collection of Mr. and Mrs. W. F. Higgins at Croydon where most of them had been growing for at least 15 years.)

LINNEAN SOCIETY.

1. Silver Medal, struck in 1746 for Count Tessin, to whom Linnaeus dedicated the 1st volume of the 10th edition of the *Systema*.
2. Silver Medal by Ljungberger, struck by command of Gustavus III in 1778.
3. Seals of Jonas Dryander, Robert Brown and Sir James Edward Smith.
4. Seal with bust of Linnaeus engraved by Tassie.
5. Gold Medal presented to J. E. Smith, 'student of physick', by Prof. J. Hope, Edinburgh, 1783.
6. Portrait of Johann Hedwig (1730-1799) mounted in a ring.
7. Commonplace Book of Peter Collinson open at an entry relating to Richard Beauchamp, Earl of Warwick, Lord Despenser of Burgundy, ob. 1439, and showing the lock of the Earl's hair referred to at the foot of the page.

THE FRESHWATER BIOLOGICAL ASSOCIATION, WINDERMERE LABORATORY.
Lake District Ephemeroptera and Trichoptera. [Shown by Dr. T. T. MACAN and Miss E. E. SANDISON.]

(*Siphonurus lacustris* occurs in the slow reach of the beck on the mountain top. In the torrential portion there are six common species: *Ameletus inopinatus*, *Ecdyonurus torrentis*, *Rithrogena semicolorata*, *Baëtis rhodani*,

Baëtis pumilus and *Ephemerella ignita*. The first extends down only to a point about 1,000 feet above sea level and is thought to be a cold-water species.

Although the river may have a stony bottom just like that of the beck, there are certain interesting and inexplicable differences in its fauna. *Ecdyonurus torrentis* is largely replaced by *E. dispar*. The two beck species of *Baëtis* persist but they are joined by a third, *B. scambus*, which is often the commonest of the three.

As the river becomes more sluggish, silt is deposited and rooted vegetation establishes itself. Except *Ephemerella ignita*, the species of Ephemeroptera characteristic of fast flow and a stony substratum disappear. *Baëtis niger* and *Cloeon dipterum* are two common weed-species.)

(Larvae inhabiting becks counteract the risk of being washed away in one of two ways; *Rhyacophila dorsalis* and the Polycentropids are free-living and cling to stones with stout claws, whereas *Chaetopteryx villosa*, *Silo pallipes*, *Goera pilosa* and *Agapetus fuscipes* construct heavy cases of stones.

Tarn species, less in danger of being washed away, build lighter cases. Near the mouth of becks where the bottom is stony or sandy, *Goera pilosa* may again be found together with *Molanna angustata* and *Sericostoma personatum*. In deeper parts of the tarn *Mystacides* spp. and *Leptocerus aterrimus* abound on a muddy bottom, whereas *Lepidostoma hirtum* prefers *Littorella* or *Isoetes*. *Phryganea* spp., *Limnophilus rhombicus* and *L. marmoratus* live among the roots of plants bordering the tarn; *Glyptotendipes pellucidus* prefers the shade of trees, the fallen leaves of which it uses in case-building. *Trienodes bicolor* is the only larva capable of swimming; this it achieves by means of a pair of elongated hair-fringed legs.

Phryganea varia were demonstrated building their cases.)

ROYAL BOTANIC GARDENS, KEW.

1. The New Flora of Tropical East Africa. [Shown by Dr. W. B. TURRILL and Mr. E. MILNE-REDHEAD.]
2. Photographs of Tropical African Vegetation. [Shown by Mr. A. B. BULLOCK.]

The floral decorations in the Library were provided by the CHELSEA PHYSIC GARDEN.

PROCEEDINGS OF THE GENERAL MEETING ON 10 January 1952

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 22 November 1951, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Dr. Agnes Arber, F.R.S., Mrs. Nora Cox, Professor R. E. Holtum, Sir Norman B. Kinnear, C.B., Mr. Richard Morse, Mr. A. A. Prestwich, Dr. T. E. Wallis, Professor F. E. Weiss, F.R.S., and the University, Cambridge.

The PRESIDENT reported the deaths of Wilfred Mark Webb, Fellow, and John McConnell Black, Associate *honoris causa*.

The following communication was read and discussed :—

Professor J. McLEAN THOMPSON. A further contribution to our knowledge of Cauliflorous Plants; with special reference to the Candle-Tree of Panama (*Parmentiera cereifera* Seem.). (Discussed by the President, Prof. F. E. Weiss, Dr. George Taylor and Dr. R. Melville; Prof. McLean Thompson replied.)

Abstract.—

Though systematic study of the Bignoniaceae is well advanced, and some have raised the interest of anatomists, there is but scanty knowledge of their ways of growth and of their flowering modes.

The present statement is concerned with one tree-form attained, and with some steps in adult growth which lead to cauliflory. The plant discussed is one in which sympodial growth prevails till sapling life is past, and is subordinate in later life, once flowering has begun. In time, it blossoms frequently from close beneath its crown to low positions on its bole, no distance from the ground. Its cauliflory thus exceeds by far that shown by allied plants which have been studied partially, though not in sapling life (The Sausage-Tree and the Calabash-Tree).

Some features of its body-growth are briefly reviewed, as giving contrast to prevailing ones once flowering-time has come. Then many lateral buds mature as stumpy leafy spurs which may be later lengthened as foliar shoots or suckers, with crowded basal resting buds which play a part in flowering. In chief, the latter may be traced to spur-shoots, brought to rest, and then reduced by absciss-layers to stumps with basal buds. As nodes grow broad, these stumps are sunk in narrow deepening pits; and buds they bear form single flowers or minor hidden branches. All sunken flowers are then exposed by lengthening from the pits and prove most often fertile, with fruits matured in full. The lateral branches gain in length in later flowering seasons, and lose their tips at absciss-layers, once awl-shaped leaves have formed. The basal buds on sucker-shoots and upper leafy branches bear first quite tiny awl-shaped leaves, placed mainly distally. They rarely gain in length or breadth and may be soon excised: some leave short stumps with crowded scales and single axial buds. The latter lead to single flowers and further sunken shoots so that branch-bases, too, may bloom through many later years. This tree flowers first on branch-tips within its forming crown and later on quite perfect spurs, at slightly lower levels. It keeps these spurs undamaged till fruit has partly formed. First flowers exposed are often small and rarely carry stamens: their fruits are seldom full-matured and may be much deformed. In the course of time, new flowering comes at ever-lowered levels till dormant buds on basal shoots are actively involved. These buds are lower ones of axial pairs which seedling plants had borne: their close and upper neighbours had formed sympodial branches.

In that the flowering mode described relates to surface-buds, the view which Schimper took of it applies in minor part.

It will appear that flower-structure brings some doubts on floral theory but does not in itself suffice to bring new certainty.

PROCEEDINGS OF THE GENERAL MEETING ON 24 January 1952

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 10 January 1952, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. V. Bogdan and Dr. E. E. Sherff.

The PRESIDENT invited Fellows of the Society to send nominations for Officers, New Members of Council, Foreign Members and Associates *honoris causa* to the General Secretary by 20 February next.

The PRESIDENT reported that the Royal College of Surgeons had invited Members of the Linnean Society to be present at the church of St. Martin-in-the-Fields at 11 a.m. on 14 February 1952, when Sir Henry Dale, F.R.S., would unveil a tablet to commemorate the fact that John Hunter's remains rested there from 1793–1859.

Certificates of recommendation for election to Ordinary Associateship were read for the first time in favour of :—Kenneth L. Alvin, B.Sc., Raymond Harvey, B.Sc., and Miss Alice Barbara Patricia Stevens, B.Sc.

The following communication was read and discussed :—

Dr. E. B. EDNEY. The Woodlice of Great Britain and Ireland. (Discussed by the President, Dr. C. F. A. Pantin, Dr. A. Tindell Hopwood and Dr. J. L. Cloudsley-Thompson ; Dr. Edney replied.)

THE WOODLICE OF GREAT BRITAIN AND IRELAND

A concise systematic monograph

By E. B. EDNEY

(from the Zoology Department, Birmingham University).

(With 164 text-figures and 2 diagrams.)

(Communicated by Dr. I. Gordon, F.L.S.)

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INTRODUCTION.

Nearly half a century has elapsed since the publication in 1906 of Webb & Sillem's *British Woodlice*, and although there has been a great deal of literature on the subject since then, their book has remained the standard English work of reference. The late Dr. W. E. Collinge, who contributed much to our

knowledge of the natural history and systematics of the group, promised a monograph for some years, but was unable to write it before he died in 1948.

The writer was led to undertake the present work primarily as a result of difficulty experienced in identifying woodlice for use in physiological work. 'Webb & Sillem' is out of date (and has been out of print for many years), and more recent literature is scattered throughout a number of journals not at all easy of access. Furthermore, an examination of this literature shows several disturbing discrepancies between British and continental work—indeed, a great deal which has been done on the continent, particularly by Verhoeff and Vandel, appears to have gone unnoticed in this country. (See, however, Ellis (1941).)

The present work, then, is an attempt to bring the British and Irish faunal list up to date and the nomenclature into line with modern practice; it is intended as a structural skeleton rather than an exhaustive systematic monograph.

Without attempting to summarize all the systematic literature since the time of Webb & Sillem, some of the more important works, so far as British Isopods are concerned, may briefly be mentioned. New species have been described by Patience, Bagnall, Collinge and others (references under the species concerned) and other species, known from abroad, have been added to the list, so that whereas Webb & Sillem described 25 species, the list now includes 38. The American species, several of which occur also in Britain, have been admirably monographed by Van Name (1936), and Spengel's monograph (1932, 34) of the Danish species is very valuable. The Irish species were listed by Beresford & Foster (1911) whose paper includes keys and data on distribution, but the species are not described and only two are figured. Collinge (1918) published an annotated check-list of the British species. He also published a large amount of information on their distribution, much of which is summarized in his paper on that subject published in 1943. A large number of new 'varieties' were also described by Collinge: they are mainly colour varieties, and without further experimental and ecological investigation it is impossible to assess their systematic status. The type material of many of these varieties has been examined, and there appear to be no morphological features distinguishing them from the typical species concerned, and it is best to neglect them as systematic units until such time as their validity may be confirmed. They are therefore not included in the main body of the present work, but are listed in an appendix.

A very useful genetical approach to the problem has been made by Howard (1940, 1947) and also by Vandel (1934, 1945 and other papers) and Legrand, Strouhal & Vandel (1950). These workers have investigated the genetics of certain colour varieties and the inheritance of monogeny (the production of offspring of one sex only). Complete or partial monogeny is known to occur in *Armadillidium vulgare*, *Trichoniscus pusillus*, *Ligidium hypnorum* and other species; its mode of inheritance, whether cytoplasmic or by the Y-chromosome (females being the heterogametic sex) is uncertain.

From the systematic point of view, several advances have been made during the present century, both in taxonomic grouping and in methods of description. In particular the old genera *Trichoniscus* Brandt and *Philoscia* Latreille, have been shown to be heterogeneous groups and divided into a number of separate genera by Verhoeff (1908 a, b, c, etc.), Racovitza (1907, 1908), Graeve (1914) and Kesselyak (1930). Perhaps the most cogent reason for these reorganizations lies in the structure of the male genitalia (modified 1st and 2nd pleopods), which have been shown to be of great systematic significance; but other structural features associated with the nature of the integument, the structure of the mouth parts, the development of epimera

and particularly the development of secondary sexual characters, such as the modification of the last pair of pereopods into claspers (Vandel, 1950 a), all point in the same direction. Vandel (1943) has published a review on the origin and evolution of terrestrial Isopods in which the significance of these and other features is assessed.

Several genera have lately received monographic treatment particularly by Vandel and Legrand—these will be noticed under the genera concerned.

Investigations into the physiology and behaviour of the group have also been made, and this has proved to be a fertile field, as indeed might be expected, since the *Oniscoidea* are the only Crustacean animals to have successfully occupied a terrestrial habitat; but this is not the place to survey the literature which has accumulated on that side of the problem.

METHODS OF DESCRIPTION.

It has already been mentioned that the present work does not claim to be more than a systematic summary of the British and Irish species. The descriptions given of the genera and species are not therefore exhaustive. The aim has been to make identification reasonably certain, and illustrations are used rather than lengthy verbal description, particularly of the male genitalia, whose taxonomic value is considerable. Diagram 1 illustrates the terminology used in the present work.

The terms 'pereion' and 'pleon' are used in preference to 'thorax' and 'abdomen', to avoid undesirable associations; the homely term 'head' has been used, since there is no mistaking its meaning, in preference to the more correct 'cephalon'; it refers to that part of the animal anterior to the pereion, and morphologically includes the 1st 'thoracic' somite, which bears the maxillipeds.

The lateral expansions of the trunk somites are referred to as 'epimera': they may fall into line with the general convexity of the dorsal surface of the animal, or they may be bent outwards, when they lie in a more or less horizontal plane, in which case they are described as 'laterally expanded'. The relative development of the epimera of the pleon is a character of taxonomic value. In some genera the posterior margin of the pereion is wider than the anterior margin of the pleon, so that the general outline of the animal, instead of being continuous, is broken at the junction of the two regions. This is a clear-cut difference and is a feature of taxonomic importance.

The antennules, or 1st antennae, are universally present but usually minute, and they are not used in the specific descriptions, neither are they figured. The term 'antenna' refers to the large 2nd antenna, whose structure is of great taxonomic value, particularly as regards the number of segments in the flagellum, and their relative lengths. The peduncle consists always of five segments, and the proportions of the last of these have been used as a specific character. In all families except the Trichoniscidae the flagellar joints are distinct, but in that family it is often difficult to be quite sure how many segments are present; in spirit specimens it is helpful to allow the animal to dry, but a cleared microscopic preparation is preferable. In measuring the various segments, the width is taken at the widest part; the length is simple to measure unless the segment is bent in relation to its proximal neighbour, and then the length is taken from the middle of the distal margin of the next proximal segment. The ratios of relative lengths and widths do vary intra-specifically to some extent and they are unreliable in young specimens, but in the experience of the writer, measurements can be found with little or no inter-specific overlap. Variability, when present, is mentioned in the descriptions.

The shape of the exo- and endopodites of the uropods is also used as a specific character. For the most part there can be little ambiguity as to the

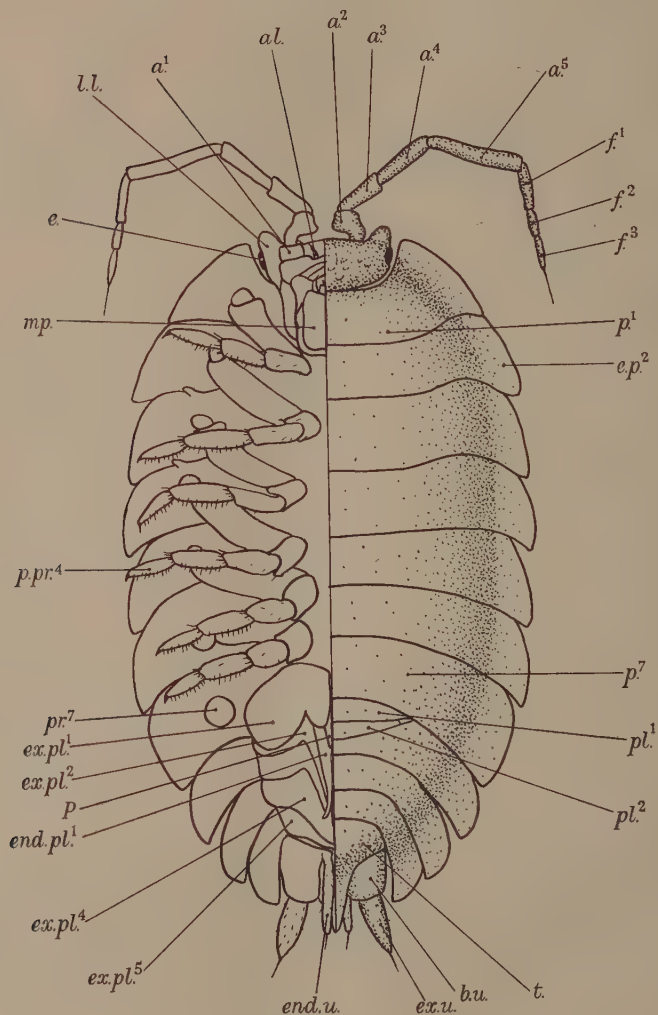


DIAGRAM 1.—*Oniscus asellus* L., semi-diagrammatic, to show the terminology used. Right half, dorsal surface; left half, ventral surface. a^1 – a^5 , 1st to 5th joints of the peduncle of the antenna; al , antennule; $b.u.$, basipodite of the uropod; e , eye; $e.p^2$, epimeron of the 2nd pereonite; $end.pl^1$, endopodite of the 1st pleopod; $end.u.$, endopodite of the uropod; $ex.pl^1$ – $ex.pl^5$, exopodites of the 1st to 5th pleopods; $ex.u.$, exopodite of the uropod; f^1 – f^3 , 1st to 3rd segments of the flagellum of the antenna; mp , maxilliped; ll , lateral lobe of the head; P , 'penis'; p^1 and p^7 , 1st and 7th pereonites; pl^1 and pl^2 , 1st and 2nd pleonites; $p.pr^4$, propodite of the 4th pereopod; pr^7 , position of the 7th pereopod (removed to display the pleopods); t , telson.

measurement made—it may be as well to stress that it is only the distal segment which is measured—at first sight the exopodite may appear two-segmented in some species, the proximal part is of course part of the basipodite. The width of the base of the telson, where stated, is measured between the points at which the lateral margins of the telson disappear under the previous segment.

DISTRIBUTION.

It is not proposed to include detailed locality data in the present monograph. The distribution of each species will be indicated in general terms, and in the case of rarer species, recorded from only a few localities, the counties will be mentioned. Further information is available for Great Britain in Collinge (1943), and (although rather out of date) for Ireland in Beresford & Foster (1911). Collinge also published much information upon detailed distribution of individual genera and species in the *North Western Naturalist*, particularly from 1940 onwards.

As regards what may be called the 'micro-distribution' of woodlice, much remains to be discovered. Little can be said beyond the fact that certain genera such as *Ligia* and *Halophiloscia* are littoral or near littoral, that others such as the Trichoniscidae, inhabit very damp situations, that *Armadillidium* occurs in apparently drier micro-climates, and that other genera are intermediate. Even these generalities are open to question, for it is common to find Trichoniscids, Porcellionids and Armadillidiids all living in the same rubbish heap; and we really know very little about the precise conditions obtaining in the so-called 'dry' micro-habitats of *Armadillidium* or *Porcellio*. It is in this field, where ecology and physiology overlap, that more investigation is needed (vide Edney, 1951 a, b, 1952). Little known also as regards the relation between soils and woodlouse distribution, though the high calcium content of the integument might be expected to cause considerable sensitivity to soil constitution.

ACKNOWLEDGMENTS.

It is a pleasure to acknowledge the help and guidance received from Prof. A. Vandél, of the University of Toulouse, who not only provided me with European material for purposes of comparison, but directed my attention to several *points litigieux* in the literature of British woodlice, and to many sources of information. I am also indebted to Dr. I. Gordon, of the British Museum, for the loan of material, for facilities in her department, for much valuable advice and for reading the manuscript. I have also been able to use the Collinge collection through the kindness of Mr. G. F. Willmot, Curator of the Yorkshire Museum. Mr. H. J. Larwood, of Liverpool University, also lent me material from his collection. Lastly I should like to thank all those who have from time to time collected for me, who are too numerous to mention individually; I am most grateful for their assistance.

SYSTEMATIC SECTION.

Key to the British Families and Genera.

- | | |
|--|-------------------------|
| 1. Flagellum of antenna with ten or more segments (fam. Ligidae) | 2. |
| — Flagellum with less than ten segments | 3. |
| 2. Outline of pereon and pleon continuous; large animals, up to 30 mm. long | <i>Ligia</i> Fabricius. |
| — Base of the pleon narrower than the pereon, making a distinct break in the outline; smaller animals, 6–10 mm. long | <i>Ligidium</i> Brandt. |

3. Eyes absent or composed of up to three ocelli; flagellar segments usually more than three, often indistinct; inner and outer rami of the uropods similar in shape (fam. Trichoniscidae)..... 4.
- . Eyes present (except in *Platyarthrus*) and compound (or if simple, as in *Eluma*, then the animal capable of rolling into a ball); flagellum of up to three distinct segments; exopodites of the uropods usually much broader than the endopodites 10.
4. Outline of pereion and pleon continuous, tergites of the former with longitudinal ridges or rows of tubercles (see figs. 52, 56) (subfam. Haplophthalminae)..... *Haplophthalmus* Schöbl.
- . Base of the pleon narrower than the pereion, tergites without longitudinal sculpture (subfam. Trichoniscinae) 5.
5. Eyes absent or composed of a single ocellus; left mandible with three, right with two penicils behind the cutting edge (fig. 51); exopodite of the 1st male pleopod bearing two fine processes posteriorly (figs. 16, 20) *Trichonoscoides* Sars.
- . Eyes of one or three ocelli; left mandible with two, right with one penicil (except *Oritoniscus* which has three and two respectively); exopodite of the 1st male pleopod without a posterior process or with only one. 6.
6. Eyes with a single ocellus 7.
7. Eyes with three ocelli 9.
7. Surface smooth, flagellum with five or more segments; exopodite of 1st male pleopod with a deep rounded excision near the inner end of the posterior margin, and a single strong process median to this (fig. 46)..
- Surface tuberculate; flagellum with less than five segments; exopodite of 1st male pleopod without such excision or process..... 8.
8. Endopodite of the 1st male pleopod long and tapering, the inner margin of the 2nd exopodite finely toothed (figs. 42, 43). Body fully 3.5 times as long as wide; apical margin of the telson feebly convex; 'penis' without minute teeth *Miktoniscus* Kesselyak.
- . Endopodite of the 2nd male pleopod spoon-shaped apically, the 2nd exopodite without teeth; broader animals; the sides of the 'penis' minutely toothed near the apex (fig. 38) *Androniscus* Verhoeff.
9. 'Penis' club-shaped towards the tip, apical segment of the endopodite of the 1st male pleopod reduced to a long tapering filament (figs. 30, 34) *Cordioniscus* Graeve.
- . 'Penis' tubular, becoming gradually narrower apically; apical segment of the 1st male endopodite well developed, as wide at the base as the basal segment (figs. 11, 24) *Trichoniscus* Brandt.
10. Endopodites of the uropods projecting when the animal walks, and normally visible from above..... 11.
- . Endopodites of the uropods not projecting and normally invisible from above, except sometimes the extreme tips. (In *Eluma* they are exposed by the short telson, but then the eyes are simple) (fam. Armadillidiidae.) 18.
11. Pseudotracheae absent (fam. Oniscidae) 12.
- . Pseudotracheae present on at least some of the pleopods (fam. Porcellionidae) 16.
12. Outline of the pleon and pereion discontinuous 13.
- . Outline of the pleon and pereion continuous..... 15.
13. Telson pointed apically (fig. 68), tergites glabrous *Philoscia* Latreille.
- . Telson rounded, tergites with sparse hairs..... 14.
14. Endopodite of the 1st male pleopod wide throughout its length, with a lateral projection apically (fig. 63); exopodites of the uropods more than four times as long as the endopodites (fig. 62) *Halophiloscia* Verhoeff.
- . Endopodite of the 1st male pleopod tapering in the distal half (fig. 73); exopodites of the uropods not more than twice as long as the endopodites *Chaetophiloscia* Verhoeff.

15. Eyes absent, the proximal of the two flagellar segments extremely short (fig. 78) ; myrmecophiles *Platyanthrus* Brandt.
 -. Eyes present, 1st flagellar segment well developed (fig. 82) *Oniscus* Linné.
 16. Able to roll into a ball *Cylisticus* Schnitzler.
 -. Unable to roll into a ball 17.
 17. Base of the pleon narrower than the pereion *Metaponorthus* Budde-Lund.
 -. Outline of the pereion and pleon continuous *Porcellio* Latreille.
 18. Eyes single, telson not nearly reaching the tips of the uropods (fig. 162) *Eluma* Budde-Lund.
 -. Eyes compound, telson reaching or nearly reaching the tips of the uropods (figs. 127, 132, 147) *Armadillidium* Brandt.

Family **Ligiidae** Sars, 1898.

Genus **LIGIA** Fabricius, 1793.

Characters.

Body regularly oblong oval, feebly convex above, the margin of the pleon continuous with that of the pereion ; epimera well developed, particularly on the pleon. Eyes large and compound ; antennae long, flagella multi-articulate. Head without lobes. Legs increasing in length posteriorly, the last segment of each bi-unguiculate. Uropods wholly visible from above, the rami styliform, nearly equal in length. Mandibles with numerous penicils behind the cutting edge. Vasa deferentia each opening at the end of a separate process, endopodites of the 1st male pleopods not modified into copulatory appendages, those of the 2nd pair strongly elongate (figs. 3, 4). Pseudotracheae absent.

One British species.

Ligia oceanica (Linné). (Figs. 1-4.)

Oniscus oceanicus Linné, 1767.

Cymothea oceanica Fabricius, 1793.

Ligia scopulorum Leach, 1815.

Characters.

The largest of the British woodlice, up to 30 mm. long, rather more than twice as long as broad. Greenish grey, with black eyes. Head 2.2 times as wide as long. Flagellum with 11 to 15 segments ; antennae without conspicuous spines, the last segment of the peduncle about seven times as long as wide. Tergites with many small, irregularly arranged tubercles ; pleon epimera produced backwards, acuminate. Telson broadly rounded behind. Rami of the uropods more than ten times as long as wide at the base.

Distribution.

This species is restricted to the coastline, where it occurs in crannies above high tide mark. It occurs all round the British Isles.

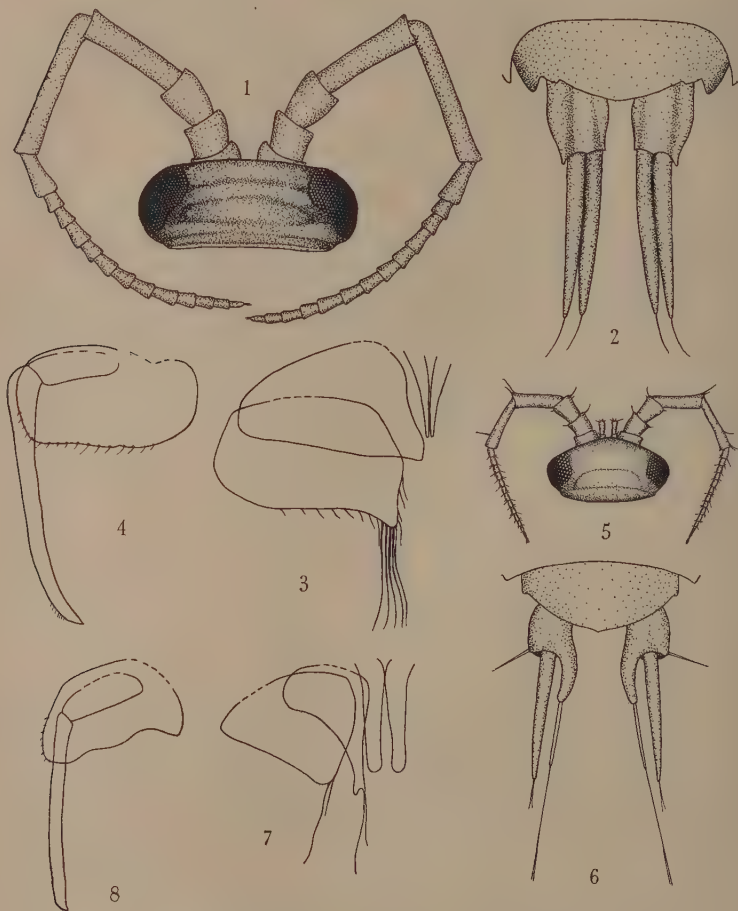
Genus **LIGIDIUM** Brandt, 1883.

Characters.

Body oblong oval, the base of the pleon narrower than the pereion ; strongly convex above. Epimera well developed but not expanded horizontally. Eyes large and compound. Antennulae conspicuous, much stronger than in *Ligia*, antennae not so long as in *Ligia*, the flagellum multi-articulate. Head without lobes. Legs greatly increasing in length posteriorly, each terminal segment with a single claw. Uropods wholly visible from above, their rami unequal in length. Mandibles each with three penicils behind the cutting edge. Vasa

deferentia each opening by a separate process, endopodites of the 1st male pleopods unmodified as copulatory appendages, those of the 2nd pair strongly elongate. Pleopods without pseudotrachae.

One British species.



FIGS. 1-4.—*Ligia oceanica* (Linné). 1, head, $\times 8$; 2, telson and uropods, $\times 8$; 3, 1st σ pleopod and 'penis', $\times 13$; 4, 2nd σ pleopod, $\times 13$.

FIGS. 5-8.—*Ligidium hypnorum* (Cuvier). 5, head, $\times 13$; 6, telson and uropods, $\times 13$; 7, 1st σ pleopod and 'penis', $\times 28$; 8, 2nd σ pleopod, $\times 28$.

Ligidium hypnorum (Cuvier). (Figs. 5-8.)

Oniscus hypnorum Cuvier, 1792.

Oniscus agilis Persoon, 1793.

Ligia hypnorum Bosc, 1830.

Zia saundersii Stebbing, 1873.

Zia agilis Koch, 1840.

Ligidium agile Norman, 1873.

Characters.

Up to 11 mm. long, rather more than twice as long as wide. Colour variable, often a pale ochre with irregular dark brown patches, the latter becoming continuous in a line near each side of the pereion. Antennae with a small number of distinct spines, last segment of the peduncle five times as long as wide at the base; flagellum with about 12 segments, the last terminated by a brush. Head nearly twice as wide as long, its surface and that of the rest of the animal smooth; epimera of the pleon produced backwards, acuminate; telson broadly rounded behind; exopodite of the uropods four times as long as the endopodite and eight times as long as wide at the base. Endopodites of the 1st male pleopods narrowly produced posteriorly, tipped with a pair of long whip-like setae, the corresponding exopodites also with a pair of such setae; the 2nd endopodite some 15 times as long as wide.

Distribution.

The species is restricted to damp environments and has been found as far north as Lancashire, it has not been recorded from Ireland or Scotland.

Family **Trichoniscidae** Sars, 1898.

This family was established by Sars to receive the genera *Trichoniscoides*, *Trichoniscus*, *Haplophthalmus*, *Scyphacella* and *Actoniscus*, all of which were previously included in the family Ligiidae. Since that time a number of other genera have been added to the family, largely by a division of *Trichoniscus*. These additions have been made by continental workers, notably Racovitza, Verhoeff, Kesselyak and Vandel, and the family has been divided by Verhoeff (1908) and Racovitza (1908), into two subfamilies, *Trichoniscinae* and *Haplophthalminae*. For the reasons stated in the introduction, this arrangement will be followed in the present monograph. Vandel (1946, 1952) has revised the classification of the family.

Characters.

Small animals, usually less than 6 mm. long, elongate as compared with the Ligiidae. Epimera usually not strongly developed, the base of the pleon narrower than the pereion (except *Haplophthalmus*). Head usually with lateral lobes; antennae usually spinose with a small number of flagellar segments (usually three or four), the articulations often indistinct. Eyes absent or composed of one to three ocelli. Mandibles with a small number of penicils behind the cutting edge. Legs not greatly elongated, coarsely spinose. Uropods with the endo- and exopodites similar in shape and entirely visible from above. Pleopods without pseudotracheae, the 1st and 2nd pairs in males often strongly modified as copulatory appendages. The two vasa deferentia opening by a single process known as the 'penis'. Pseudotracheae absent.

Subfamily *TRICHONISCINAE* Verhoeff, 1908 a.Genus *TRICHONISCOIDES* Sars, 1898.*Characters.*

Vandel (1946 a, b) has written a valuable account of the characters of this genus. These may be briefly summarized as follows:

The genus contains the smallest of terrestrial isopods: *T. saeroensis* Lohmander (a Swedish species) measures as little as 2 mm. The colour is usually pale pink or white. Both the British species have a single ocellus on each side of the head, though this is often poorly developed in *T. albidus* Budde-Lund, and may even be invisible in preserved specimens. Left mandible with three, right with two penicils behind the cutting edge, the mouth parts

very uniform. Dorsal surface with more or less conspicuous tubercles and scales. Epimera poorly developed, not expanded horizontally. 1st and 2nd pleopods of the males strongly modified as copulatory organs, the exopodite of the 1st bears two ciliated processes at the median posterior corner, and the endopodite bears one. Head with prominent lateral lobes. Rami of the uropods visible, the exopodites wider than the endopodites but essentially of the same shape.

Remarks.

There are two British species, *albidus* Budde-Lund and *sarsi* Patience. A third species, *scabrous*, has been described by Collinge (1917), but I have not been able to trace the type or any reliably named material. Collinge's description is inadequate, not illustrated, and this must remain a *species incerta*.

Key to the species of *Trichoniscoides*.

1. Last peduncular segment of antenna three and a half times as long as wide, the flagellum of four segments *albidus* (Budde-Lund).
- Last peduncular segment barely more than twice as long as wide, the flagellum of three segments *sarsi* Patience.

Trichoniscoides albidus (Budde-Lund). (Figs. 13–17.)

Trichoniscus albidus Budde-Lund, 1879; nec *Trichoniscoides albidus* Sars, 1898.

Characters.

3.5–5.0 mm. long, three times as long as wide. Living specimens are red, but the colour is almost completely lost in alcohol (hence, presumably, the name). Antennae with a small number of distinct spines and a small number of low, minutely scaled tubercles, particularly on the last peduncular segment; the latter three and a half times as long as wide at the base; flagellum of four rather indistinct segments, the last terminated by a long, fine brush. Head twice as wide as long; its surface, together with that of the rest of the body, bears a number of irregularly arranged, minutely scaled tubercles. Body strongly convex above, its sides parallel for the greater part of their length. Posterior angles of the epimera well produced backwards; the pleon, however, without well-developed epimera. 7th male pereopod unmodified. Telson abruptly truncate apically. Rami of the uropods in the form of tapering cones, the exopodites four times as long as wide at the base, about one and a half times as long as the endopodites. 1st and 2nd male pleopods illustrated in figs. 16 and 17.

Distribution.

The species is recorded from many counties throughout the British Isles; the Irish records (Beresford & Foster, 1911), however, probably refer to *T. sarsi* Patience.

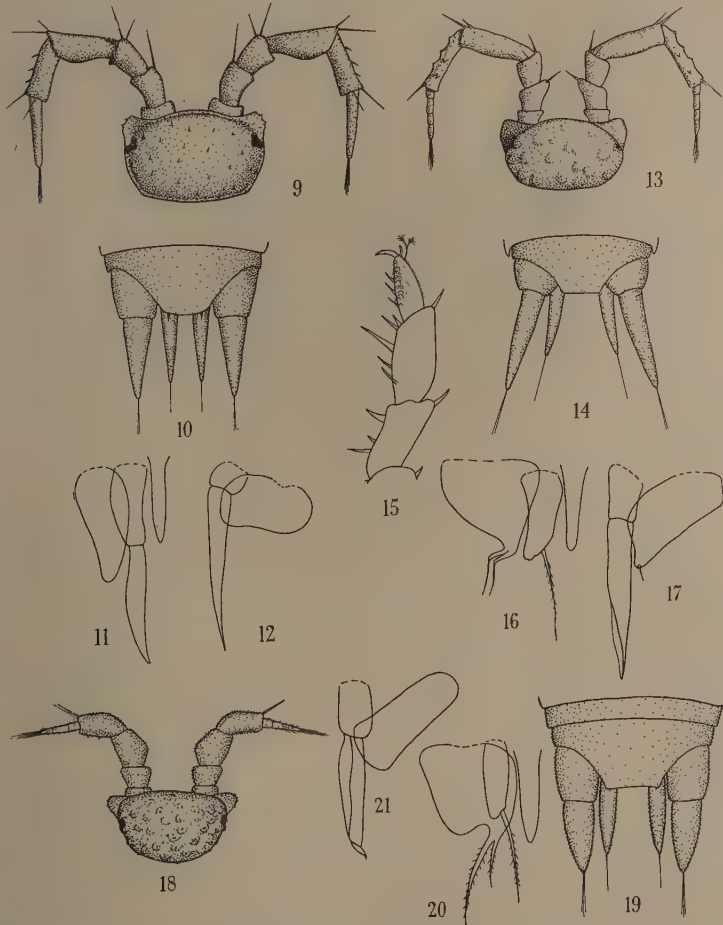
Trichoniscoides sarsi Patience, 1908 a. (Figs. 18–21.)

Trichoniscoides albidus Sars, 1898.

Characters.

3.0 mm. long, three times as long as wide. Living specimens light reddish brown, with lighter yellow patches (from Patience, 1908), preserved specimens yellowish white. Antennae much shorter than in *albidus*, similarly armed with spines and tubercles, the last segment of the peduncle hardly more than twice as long as wide; flagellum of three short segments, terminated

by a fine brush whose length is nearly as great as that of the flagellum. Head rather more than twice as wide as long, its upper surface, together with that of the rest of the body, with a number of irregularly arranged, scaled tubercles. Eyes of one ocellus each. Lateral lobes of the head well developed. Body rather more elongate than *albidus*, strongly convex above, the epimera well



FIGS. 9-12.—*Trichoniscus pygmaeus* Sars. 9, head, $\times 40$; 10, telson and uropods, $\times 40$; 11, 1st δ pleopod and penis, $\times 68$; 12, 2nd δ pleopod, $\times 68$.

FIGS. 13-17.—*Trichoniscoides albidus* (Budde-Lund). 13, head, $\times 40$; 14, telson and uropods, $\times 40$; 15, 7th δ pereopod, $\times 68$; 16, 1st δ pleopod and penis, $\times 68$; 17, 2nd δ pleopod, $\times 68$.

FIGS. 18-21.—*Trichoniscoides sarsi* Patience. 18, head, $\times 68$; 19, telson and uropods, $\times 68$; 20, 1st δ pleopod and penis, $\times 108$; 21, 2nd δ pleopod, $\times 108$.

developed on the pereion, but not expanded laterally, the posterior angles rounded. Epimera of the pleon weak. Lateral margins of the body apparently minutely denticulate. Telson truncate behind. Rami of the uropods shorter and stouter than in *albidus*, the exopodites barely three times as long as wide at the base, the endopodites shorter and about half as wide.

The male genitalia differ significantly from those of *albidus*, they are illustrated in figs. 20 and 21.

Distribution.

The species is recorded from a number of counties throughout England and the south of Scotland. It is usually associated with river banks or the seashore. Records of *T. albidus* from the coastal counties of Ireland (Beresford & Foster, 1911) may refer to *sarsi*.

Genus TRICHONISCUS Brandt, 1833.

Spiloniscus Racovitza, 1908.

Characters.

This and the following genera of the Trichoniscinae are fairly similar in general morphology, and this has been described for the family, so that only those characters which distinguish one genus from another will be considered.

Integument with minute scales, eyes each of three small ocelli, flagella of the antennae (in the British species) with four segments. Left mandible with two penicils, right with one, behind the cutting edge. Head with well-developed lateral lobes. Endopodites of the 1st male pleopods of two segments, the distal narrowing apically to a fine point and rather longer than the proximal segment; those of the 2nd pair of pleopods also two-segmented, the distal segment several times longer than the proximal, and tapering to a fine point.

Key to the species and subspecies of Trichoniscus.

- | | |
|---|--|
| 1. Dorsal surface smooth, flagellum with four segments, apical margin of the telson feebly concave. Up to 4.0 mm. long | 2. |
| -. Dorsal surface with minute scale-like hairs, apical margin of the telson convex. Up to 2.5 mm. long. | <i>pygmaeus</i> Sars. |
| 2. Colonies almost entirely of females, parthenogenetic and triploid (the very rare males sterile). Exopodite of the 1st male pleopod as in fig. 26 | <i>pusillus pusillus</i> (Brandt). |
| -. Males and females both present, reproducing sexually. Exopodite of the 1st male pleopod as in fig. 24.... | <i>pusillus provisorius</i> (Racovitza). |

Trichoniscus pygmaeus Sars, 1898. (Figs. 9-12.)

Characters.

Length 2.0-2.5 mm., three times as long as wide. Colour, whitish with a few light brown markings. Antennae of medium length, with a few long spines and a row of three smaller ones along the last peduncular segment; the latter two and a half times as long as wide. Flagellum of three indistinct segments, terminated by a fine brush. Head nearly twice as wide as long, the lateral lobes small, their margins feebly toothed. Eyes each of three ocelli. Dorsal surface of the head and body with a large number of minute scale-like hairs. Apical margin of the telson feebly convex, with a long fine spine near either end. Rami of the uropods stout and conical, the exopodites two and a half times as long as wide at the base, the endopodites only half as wide as the exopodites. Epimera of the pleon strongly produced backwards, their ends rounded, their margins, together with those of the pereion, apparently minutely dentate due to the numerous fine hair-like scales. The male genitalia are illustrated in figs. 11 and 12.

Distribution.

There are records of *T. pygmaeus* in several British counties, from Devon to Inverness. It appears also to be fairly widespread in Ireland.

Trichoniscus pusillus pusillus Brandt, 1833. (Fig. 26.)*Trichoniscus pusillus* Brandt, 1833.*Itea laevis* Zaddach, 1844.*Philougria celer* Kinahan, 1857; Bate & Westwood, 1868.*Trichoniscus rhenanus* Graeve, 1913.*T. esthoniensis* Herold, 1927.*T. batavus* Dahl, 1919.*Trichoniscus pusillus provisorius* (Racovitza), 1908. (Figs. 22-25.)*Trichoniscus provisorius* Racovitza, 1908.

Legrand, Strouhal & Vandel (1950) have recently summarized the evidence regarding the taxonomy of the *pusillus* group of *Trichoniscus*. They believe that the unisexual, parthenogenetic, triploid populations (with very rare, sterile males (Vandel, 1934)) which occur particularly in northern Europe, formed the material for the original description by Brandt, and further, that certain closely related, bisexual forms, *T. provisorius* Racovitza, 1908, *T. alticola* Legrand *et al.*, 1950, and *T. noricus* Verhoeff, 1917 a, must be considered as subspecies of *pusillus*. These subspecies are distinguishable in the males by minute differences in the shape of the exopodite of the 1st pleopod.

T. pusillus pusillus and *T. pusillus provisorius* both occur in Britain, and they may conveniently be described together, the differences between the exopodites are shown in figs. 24 and 26.

Characters.

Up to 4.0 mm. long, a little more than twice as long as wide. Colour, a mottled reddish brown. Antennae of medium length, with a small number of long spines, the last segment of the peduncle three times as long as wide, the flagellum with four indistinct segments, of which the 2nd is the longest, terminated by a long fine brush. Head nearly twice as wide as long, the lateral lobes well developed and each bearing marginally about four distinct spines. Body very strongly convex above, the sides parallel, sparsely beset with short hairs and (in living specimens) bearing many minute scales; epimera of the pleon well developed, produced backwards, their apices pointed. Telson with a feebly concave apical margin, the latter with two fine spines, one near each extremity. Rami of the uropods conical, the exopodites three times as long as wide at the base; the endopodites a little shorter than the exopodites and only half as wide at the base. The male genitalia are shown in figs. 24 to 26.

Distribution.

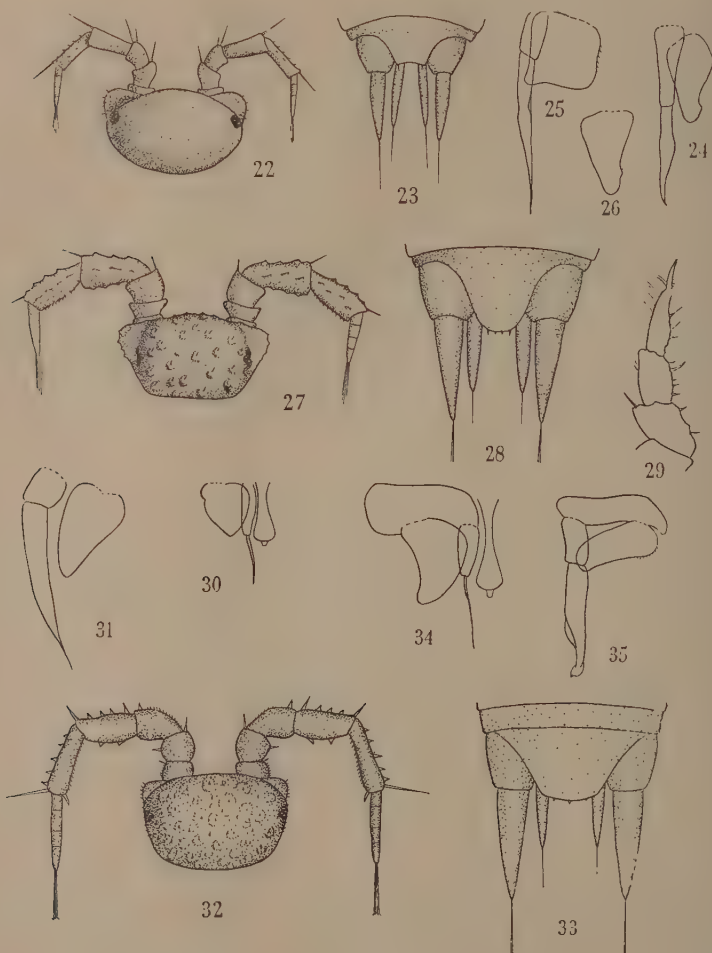
T. pusillus has been reported from most counties of the British Isles. I have seen colonies of *T. pusillus provisorius* from many of the southern counties, and Vandel believes that this subspecies occurs as far north as Lancashire. Those records further north than this are probably *pusillus pusillus*.

Genus CORDIONISCUS Graeve, 1914.

Trichoniscus Brandt, 1833, in part.*Characters.*

Integument tuberculate. Antennae spinose, flagella with four to seven segments (four in both British species). Lateral lobes of the head more or less well developed, spinose or denticulate. Eyes each of three ocelli. Left mandible with two, right with one penicil behind the cutting edge. 'Penis' single and swollen or club-shaped apically, with a short, conical

process at the extreme apex upon which the vasa deferentia open. Male pleopods: 1st exopodite approximately triangular, endopodite of two segments, the proximal in the form of a truncated cone, the distal much narrower and



FIGS. 22-25.—*Trichoniscus pusillus provisorius* (Racovitza). 22, head, $\times 28$; 23, telson and uropods, $\times 28$; 24, 1st δ pleopod and penis, $\times 68$; 25, 2nd δ pleopod, $\times 68$.

FIG. 26.—*Trichoniscus pusillus pusillus* Brandt. 1st δ pleopod (exopodite), $\times 68$.

FIGS. 27-31.—*Cordioniscus stebbingi* (Patience). 27, head, $\times 40$; 28, telson and uropods, $\times 40$; 29, 7th δ pereopod, $\times 68$; 30, 1st δ pleopod and penis, $\times 68$; 31, 2nd δ pleopod, $\times 68$.

FIGS. 32-35.—*Cordioniscus spinosus* (Patience). 32, head, $\times 40$; 33, telson and uropods, $\times 40$; 34, 1st δ pleopod and penis, $\times 68$; 35, 2nd δ pleopod, $\times 68$.

a little longer, whip-like; 2nd exopodite strongly transverse, the endopodite two-segmented, the basal segment one-third or less as long as the apical, the latter tapering distally.

Key to the species of Cordioniscus.

1. Apical margin of the telson strongly convex, with four spines ;
flagellum four times as long as wide, last peduncular segment
twice as long as wide *stebbingi* (Patience).
- . Apical margin of the telson feebly convex, with three stout
spines ; flagellum six times as long as wide, last peduncular
segment three and a half times as long as wide *spinosus* (Patience).

Cordioniscus stebbingi (Patience). (Figs. 27–31.)

Trichoniscus stebbingi Patience, 1907 a.

Characters.

Length 2.5–3.0 mm., two and a half times as long as wide. Colour in life “dark reddish brown marbled with white” (Patience, 1907 a). Antennae short and stout with a number of coarse, short spines, 2nd to 4th segments each with a longer, finer spine at the apex ; terminal segment of the peduncle twice as long as wide ; flagellum no longer than the last peduncular segment, composed of four indistinct segments and terminating in a fine brush. Head with the lateral lobes well developed, the latter with denticulate margins. Eyes of three closely set ocelli. Head above strongly tuberculate, each tubercle bearing a minute spine ; the rest of the body strongly tuberculate, the tubercles in transverse rows. Pereion strongly convex above, epimera well developed, those of the posterior segments strongly produced backwards, acuminate. Epimera of the pleon feebler. Telson with a convex apical margin, the latter armed with four short spines. Rami of the uropods conical, the endopodites half as wide at the base as the exopodites. The male genitalia are shown in figs. 30–31, they differ from those of *C. spinosus* mainly in the shape of the 1st and 2nd exopodites. 7th male pereopod unmodified.

Distribution.

This species, originally described from Glasgow, has now been recorded from as far south as the Isle of Wight as well as from Glamorgan, and the Botanic Gardens, Dublin.

Cordioniscus spinosus (Patience). (Figs. 32–35.)

Trichoniscus spinosus Patience, 1907 b.

Characters.

Similar in general shape to *C. stebbingi*. Length up to 5.0 mm., two and a half times as long as wide, the sides parallel. Colour in life as in *stebbingi*. Antennae spinose, rather longer than those of *stebbingi*, the last peduncular segment narrower than the rest, three and a half times as long as wide ; flagellum of four indistinct segments, the whole a little longer than the last peduncular segment, tipped by a long fine brush. Lateral lobes of the head less prominent than those of *stebbingi*, their lateral margins with a number of very short hairs. Eyes of three ocelli each, dorsal surface of the head less coarsely tuberculate than in *stebbingi*, the pereion similarly sculptured, the tubercles on both head and pereion bearing minute spines. Body strongly convex above, the epimera of the pereion well developed, their margins together with those of the pleon, minutely denticulate. Apical margin of the telson less strongly rounded than in *stebbingi* and bearing three very short, stout spines. Rami of the uropods conical, the exopodites rather more than three times as long as wide, the endopodites much shorter and narrower (the difference between the pairs is greater than in *stebbingi*). The male genitalia are shown in figs. 34 and 35.

Distribution.

Recorded only from Glasgow (type locality) and Edinburgh.

Genus *ANDRONISCUS* Verhoeff, 1908 b.

Trichoniscus Brandt, 1833, in part.

Characters.

Integument distinctly spinose. Eyes present or absent (in the British species, present). Antennae feebly spinose, flagella with four segments. Left mandible with two, right with one, penicil below the cutting edge. Meropodite of the 7th pereopod in males with a very strong process below, which together with the carpopodite (which is hollowed out in some species), forms a pair of pincers used in copulation (fig. 40). Male genitalia strongly modified: the endopodite of the 1st pleopod bears a spoon-shaped expansion terminally, that of the 2nd, which is apparently three-segmented, is intricately sculptured apically (figs. 38, 39). The shape of the 'penis' is very characteristic of the genus: it is rather longer than usual and towards the apex it bears a row of distinct, though minute, teeth on each side.

Remarks.

In his original description of the genus, Verhoeff pointed out that the term '*Trichoniscus roseus*' had been used by many authors to refer to what are in fact several different species. The original *Itea rosea* of Koch is an alpine species which, together with others of its group, differs from the British species in having two rows of tubercles on the segments of the pereion; further, the spoon-shaped apex of the endopodite of the 1st male pleopod is quite different in shape and transversely striated, and the teeth at the end of the 2nd endopodite are differently arranged. Verhoeff believed that the British species was *weberi* Koch, and that this was the species illustrated by Webb & Sillem (1906) as *roseus*. Since those authors did not figure the male genitalia this may have been the case, but it now appears that our common species is *dentiger*, for I have compared material with *dentiger* from Verhoeff's collection and they appear to be identical.

My attention has been drawn by Professor H. P. Moon to the type specimen of *Stenasellus hazeltoni* Collinge, deposited in the York Museum. This specimen, which was collected in August 1946 by D. A. Coase from Cheddar Gorge, Somerset, is in fact *Androniscus dentiger* Verhoeff, and bears no resemblance to the asellid genus *Stenasellus* described by Dollfus (1897, 1898). The species *Stenasellus hazeltoni* Collinge must therefore sink in synonymy.

Key to the species of Androniscus.

- | | |
|---|---------------------------|
| 1. Endopodite of the 2nd male pleopod more than seven times as long as wide at the base, its terminal segment with an inwardly directed process (fig. 39) | <i>dentiger</i> Verhoeff. |
| —, Endopodite of the 2nd male pleopod not more than six times as long as wide at the base, its terminal segment without such a process (fig. 41) | <i>weberi</i> Verhoeff. |

Androniscus dentiger Verhoeff, 1908 b. (Figs. 36–40.)

Trichoniscus roseus Sars, 1898; Webb & Sillem, 1906; non *Itea rosea* Koch, 1838.
Stenasellus hazeltoni Collinge, 1946.

Characters.

Up to 5.5 mm. long, twice to a little more than twice as long as wide. Colour in life a delicate rose-pink. Antennae fairly long, with a number of

rather short spines as well as one or two long, thin spines at the apex of each peduncular segment. Last peduncular segment four times as long as wide; flagellum as long as the last peduncular segment, consisting of four distinct segments, the 2nd longer than the others. Head one and a half times as wide as long, the lateral lobes strong, their lateral margins spinose. Eyes each of one ocellus. Dorsal surface of the head and pereion (and to a lesser extent, of the pleon) strongly tuberculate, each tubercle surmounted by a spine; the tubercles on most of the somites of the pereion arranged in three transverse rows. Trunk not so strongly convex as in other Trichoniscines; epimera well developed, those of the last somites of the pereion and the first of the pleon produced backwards and acuminate. 7th male pereopod characteristically modified (see description of genus), but the carpopodite without the concavity found in other species. Apical margin of the telson feebly concave, with a row of about four minute spines. Rami of the uropods conical, the exopodites four times as long as wide at the base, the endopodites a little shorter and narrower than the exopodites. The male genitalia are complex: they are illustrated in figs. 38 and 39.

Distribution.

Owing to the confusion in the nomenclature (see remarks under generic description) the distribution of this species is difficult to assess with certainty. Webb & Sillem's '*Trichoniscus roseus*' which includes this and the following species has been recorded from all over the British Isles, so that it is safe to assume that it is wide-spread. I have seen specimens from most of the southern counties.

Androniscus weberi Verhoeff, 1908 b. (Fig. 41.)

Trichoniscus roseus Weber, 1881; Budde-Lund, 1885; non *Itea rosea* Koch, 1838.

Characters.

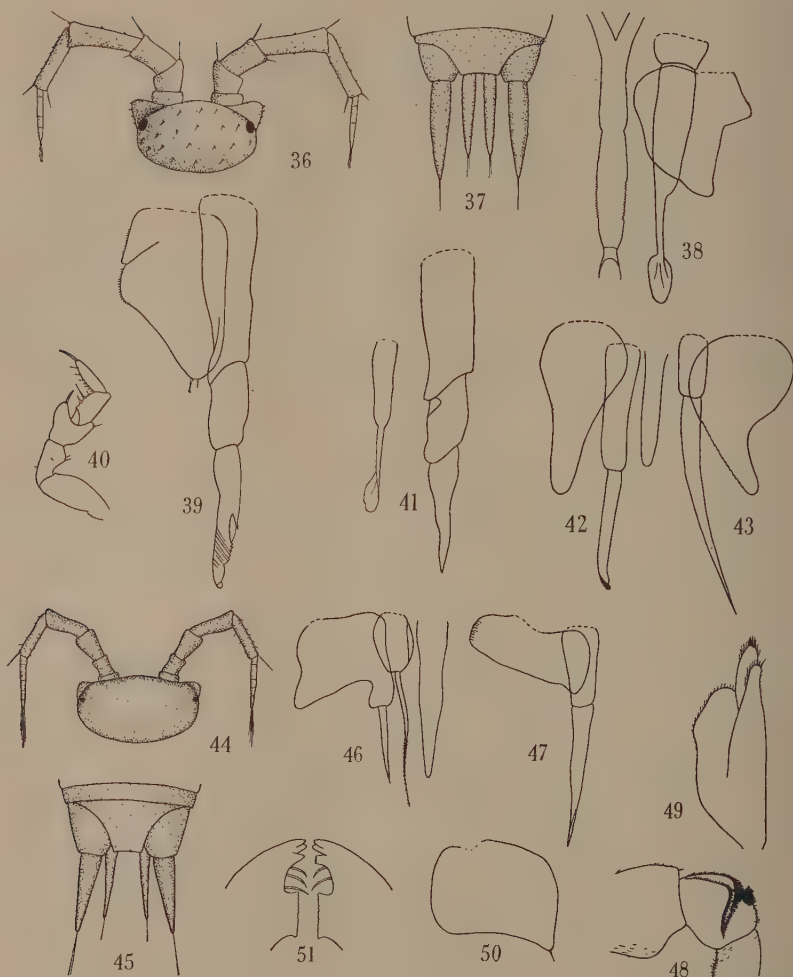
This species is essentially similar to the foregoing, differing from it in the relatively shorter male genitalia and particularly in the absence of an inward process from the middle of the terminal segment of the 2nd endopodite. These differences are indicated in fig. 41. For distribution see under *A. dentiger*.

Genus MIKTONISCUS Kesselyak, 1930.

As Vandel (1946) has pointed out, the interest of this genus (which Kesselyak established to receive the species *Trichoniscus linearis* of Patience) lies in its intermediate position between the two subfamilies of the Trichoniscidae. On the one hand, the male genitalia show distinct similarities with those of *Haplophthalmus*, yet the general body form, particularly of the epimera, which are not spread out horizontally as they are in *Haplophthalmus*, and the sculpture, is similar to that of the Trichoniscinae.

Characters.

Long narrow animals, the sides parallel, three to four times as long as wide. Left mandible with two, right with one, penicil behind the cutting edge. Eyes each of a single ocellus. Dorsal surface bearing a number of irregularly disposed, strong tubercles. Body strongly convex, epimera well developed but not expanded laterally; those of the posterior somites of the pereion strongly produced posteriorly and acuminate. Antennae spinose, their flagella of three or four indistinct segments. 'Penis' normal, cylindrical. Endopodites of the 1st male pleopods of two segments approximately equal in length, the tips pointed and curved inwards; exopodites somewhat elongated, their apices rounded (fig. 42). 2nd endopodites with



FIGS. 36-40.—*Androniscus dentiger* Verhoeff. 36, head, $\times 28$; 37, telson and uropods, $\times 28$; 38, 1st δ pleopod and penis, $\times 68$; 39, 2nd δ pleopod, $\times 68$; 40, 7th δ pereopod, $\times 28$.

FIG. 41.—*Androniscus weberi* Verhoeff. 1st and 2nd δ pleopods (endopodites), $\times 68$.

FIGS. 42-43.—*Miktoniscus linearis* (Patience) (after Patience). 42, 1st δ pleopod and penis, $\times 68$; 43, 2nd δ pleopod, $\times 68$.

FIGS. 44-51.—*Oritoniscus flavus* (Budde-Lund). 44, head, $\times 20$; 45, telson and uropods, $\times 20$; 46, 1st δ pleopod and penis, $\times 52$; 47, 2nd δ pleopod, $\times 52$; 48, ischiopodite of 2nd δ pereopod, $\times 20$; 49, maxilliped, $\times 68$; 50, 3rd δ pleopod (exopodite), $\times 52$; 51, terminal part of mandibles, $\times 68$.

the distal segment much longer than the proximal, narrowing to a long thin flagellum, exopodites minutely saw-like on their inner margins (fig. 43). 7th male pereopod with a scale-bearing area on the ischiopodite; the next two segments enlarged and coarsely spinose, often forming prehensile organs,

Miktoniscus linearis (Patience). (Figs. 42-43.)*Trichoniscus linearis* Patience, 1908 a.*Characters.*

3.0 mm. long, three and a half times as long as wide. Colour in life "white, semipellucid, the male exhibiting slight ramifications of minium-red across the segments" (Patience); preserved specimens, white. Antennae spinose, the last peduncular segment three and a half times as long as wide; the flagella of three or four indistinct segments, tipped by a fine brush. Head one and a half times as wide as long, the lateral lobes well developed. Apical margin of the telson feebly convex, armed with three minute spines. Rami of the uropods conical, the exopodites three and a half times as long as wide, the endopodites narrower and somewhat shorter. 7th male pereopod with the meropodite and carpopodite enlarged and spinose, each with one spine on the inner surface distinctly larger than the rest, that on the meropodite straight, that on the carpopodite recurved inwards.

Distribution.

The species has only been recorded, so far as Great Britain is concerned, from the type locality, Kew Gardens, in Surrey. Kesselyak, however, found it to be abundant in the Botanical Gardens at Dahlem, Germany. It appears to be native to the eastern United States of America (Vandel, 1950 b).

Genus *ORITONISCUS* Racovitza, 1908.

This genus was established by Racovitza to receive the species previously named *Trichoniscoides pyrenaeus* Racovitza, 1907, *Trichoniscus flavus* Budde-Lund, 1906, and two new species.

Characters.

Integument smooth, minutely granular or spinose. Some of the largest of all Trichoniscids belong to this genus. Eyes absent or (as in the British species) composed of a single ocellus. Antennae long, their flagella with five to ten segments. Left mandible with three, right with two, penicils behind the cutting edge (in this respect resembling *Trichoniscoides*) (fig. 51). Maxilliped as in fig. 49. 'Penis' simple, tubular. Male genitalia very characteristic of the genus: 1st exopodite quadrangular, twice as long as the 2nd, its posterior margin strongly emarginate medially, leaving a lobe at the postero-medial angle, the latter bearing a stout tapering process; the endopodite with a very short basal segment, triangular in section, its apical segment consisting of a long tapering, flagellum-like process (fig. 46). 2nd exopodite transverse, the endopodite of two segments, the apical at least as long as the basal and tapering to a point (fig. 47). 3rd exopodite as represented in fig. 50.

Oritoniscus flavus (Budde-Lund), 1906. (Figs. 44-51.)*Trichoniscus vividus* Budde-Lund, 1885 (*nec* Koch, 1840).*Trichoniscus flavus* Budde-Lund, 1906.*Trichoniscus vividus* Webb & Sillem, 1906; Collinge, 1913, 1942.*Trichoniscus vandelius* Collinge, 1945.

This is the species which is known as '*Trichoniscus vividus* (Koch)' to British authors. It is however not the original species of Koch, which was named *Itea vivida* and subsequently made the type species of the genus *Hyloniscus* by Verhoeff when he established that genus in 1908. The genitalia, maxillipeds and other structures of the species being considered are quite

different from those of any *Hyloniscus*. It is the species originally referred to '*Trichoniscus vividus*' by Budde-Lund in 1885, and subsequently named *T. flavus* by the same author after recognizing his error.

I have compared the Irish material with specimens of *O. flavus* from Vallée de la Têt, Eastern Pyrenees, kindly sent to me by Professor Vandel, and there appears to be no difference save minute ones in the shape of the male genitalia, namely, that in the material from the Pyrenees, the lobe at the postero-internal angle of the 1st exopodite is produced laterally at its posterior margin rather more than it is in the Irish material, and that the position of origin of the terminal process of the 1st endopodite differs slightly. Unfortunately there is only a single male in the Irish material available to me for examination, so that it is not possible to say whether the differences are constant. Judging by the variability in other species, the material from the two sources may be considered as conspecific.

Recently Vandel (*in litt.*) has recognized two subspecies, *O. flavus flavus* (Budde-Lund), from the Eastern and Central Pyrenees, and a new subspecies from the Western Pyrenees. The typical *flavus* is distinguished by having a modified ischiopodite of the 2nd male pereopod. I have compared the Irish material with both these subspecies (again kindly sent to me by Professor Vandel), and it agrees very well with *O. flavus flavus*. The ischiopodite concerned is illustrated in fig. 48.

Collinge (1945) recognized that the Irish material was not *Hyloniscus vividus* (Koch), and considered it to be a new species of *Trichoniscus*. His description took no account of the male genitalia however, although the classification of the family Trichoniscidae is based upon the structure of these organs. In fact the genitalia are quite different from the *Trichoniscus* type, and correspond precisely with those of *Oritoniscus*.

Characters.

Up to 7.0 mm. long, about two and one-third times as long as wide, distinctly more oval in shape than many Trichoniscids. Purplish brown in life. Antennae long, rather feebly spinose, the last segment of the flagellum six times as long as wide; flagellum of five to seven segments, the joints rather indistinct, the second longer than the rest and about two and a half times as long as wide. Head one and a half times as wide as long, the lateral lobes feeble, their surface continuous with that of the upper surface of the head, not divided therefrom by a very steep declivity. Eyes large, but each of a single ocellus. Surface of the head and pereion nearly smooth, with a few minute hairs. Body not as convex above as many Trichoniscids, the epimera well developed, their margins with a row of distinct tooth-like hairs. Pleon much narrower than the pereion, the epimera not bent laterally. Ischiopodite of the 2nd male pereopod modified, much shorter than the homologous structure in the female, bearing a dense tuft of fine scale-like hairs near the middle of the outer margin, and a shallow groove, flanked by two rows of very fine, short hairs, on the basal half of the outer margin; the groove bending inwards and the hairs becoming rather longer immediately before it reaches the tuft of scale-like hairs. Rami of the uropods long and conical, the exopodites four times as long as wide at the base, the endopodites a little shorter, but at least six times as long as wide. Apical margin of the telson truncate, feebly concave. Penis long and conical; the 1st male pleopod with a two-segmented endopodite, the 1st segment triangular in section and stout, the 2nd nearly three times longer than the 1st, flagelliform; the endopodite quadrangular with a deep emargination near the median end of the posterior margin, leaving a lobe, about one-third to one-quarter as long as the whole basal segment, at the postero-median corner, surmounted by a process which is nearly as long as the basal segment. 2nd endopodite of two segments, the basal twice as long

as wide*, the exopodite transverse, twice as wide as long, with a shallow but distinct emargination near the median end of the posterior margin.

Distribution.

Queen's County, Waterford, Carlow and Kilkenny, Eire; and Antrim, Northern Ireland. One record, from the Botanical Gardens, Birmingham (Collinge, 1913) is, as its author remarks, an isolated introduction.

The occurrence of *O. flavus* in Ireland is of interest. Up to the present, this genus has been recorded only from southern France and (one species) from Corsica. Many of the species are cavernicolous, and all save *flavus* have very limited distributions, mostly in the eastern Pyrenees and the southern border of the Massif Central (see Vandel, 1948 a, b). The species *flavus* is found throughout the Pyrenees and has invaded the Massif Central as far as Sancy. Its occurrence in Ireland confirms Vandel's statement that it is an 'expanding species'.

Subfamily *HAPLOPHTHALMINAE* Verhoeff, 1908 a.

Genus *HAPLOPHTHALMUS* Schobl, 1860.

Characters.

Small animals up to 5.0 mm. long, the integument characteristically bearing longitudinal ridges or rows of tubercles. Antennae short, flagella with three or four segments. Eyes each of a single ocellus. Lateral lobes of the head well developed. Epimera of both pereion and pleon well developed and expanded laterally to a greater extent than in the Trichoniscinae. Left mandible with two, right with one, penicil behind the cutting edge. Base of the pleon not distinctly narrower than the pereion. 7th male pereopod with the mero- and carpopodites modified into pincers, forming a clasper used during copulation (fig. 60). Endopodite of the 1st male pleopods two-jointed, the distal joint rather longer than the proximal; 2nd endopodite drawn out into a long fine process. Penis simple (figs. 54, 55, 58, 59).

Legrand & Vandel, 1950, have recently published a useful revision of the French species of this genus.

Key to the species of Haplophthalmus.

- | | |
|---|----------------------------|
| 1. Tergites with longitudinal ridges; telson convex; ridges
apparent on the 3rd pleonite | <i>mengei</i> (Zaddach). |
| - Tergites with longitudinal rows of tubercles; telson truncate
abruptly or feebly concave; ridges absent on the pleonites . | <i>danicus</i> Budde-Lund. |

Haplophthalmus mengei (Zaddach), 1884. (Figs. 52-55.)

Itea mengei Zaddach, 1884.

Haplophthalmus elegans Schobl, 1860.

Characters.

Up to 4.0 mm. long, three to three and a half times as long as wide. Colour, pale yellowish or white. Antennae short with a small number of thin spines, the last peduncular segment barely twice as long as wide; flagellum of four rather indistinct segments. Head one and a half times as wide as long (including the lateral lobes, which are very large), the anterior margin triangularly produced in the middle, its dorsal surface bearing a number of coarse tubercles; near the posterior margin the tubercles are replaced by six or eight longitudinal ridges. Anterior tergites of the pereion each with 12 longitudinal ridges, of which eight are distinct and run the whole length

* Part of the apical segment is missing in the only Irish material available to me.

of the tergite, the other two are shorter. 3rd segment of the pleon also with a single pair of ridge-like protruberances near the middle of the dorsal surface. The crest of most of the ridges mentioned bears a number of saw-like teeth. Sides more or less parallel, epimera of both pereion and pleon well developed, expanded laterally and separated from each other. Telson truncate apically, its margin feebly concave. Rami of the uropods conical, the exopodites three times as long as wide, the endopodites a little narrower and shorter.

Distribution.

This species is recorded from most British counties, and from Northern and Southern Ireland.

Haplophthalmus danicus Budde-Lund, 1879. (Figs. 56-60.)

H. elegans Budde-Lund, 1870; *nec* Schöbl, 1860.

H. mengei Weber, 1881; *nec* Zaddach, 1884.

Characters.

Up to 4.0 mm. long, three to three and a half times as long as wide. Colour, yellowish white. This species differs from *mengei* in the following respects: Flagellum clearly of three segments only, the last peduncular segment a little longer comparatively than in *mengei*. The front of the head is more sharply pointed (it is rounded in *mengei*). The longitudinal ridges of *mengei* are represented by rows of tubercles in *danicus*, and the elevations on the 3rd pleonite are reduced to vanishing point. The 7th male pereopod is more strongly modified as a clasper in *danicus*, particularly by a strong excavation in the base of the carpopodite. This, and the male genitalia which also differ significantly in the two species concerned, are shown in figs. 58-60.

Distribution.

This species appears to be as widely distributed as *mengei* except in Ireland where it has only been recorded from Dublin and Carlow counties.

Family **Oniscidae** Verhoeff, 1917 b.

Sars, 1899, in part.

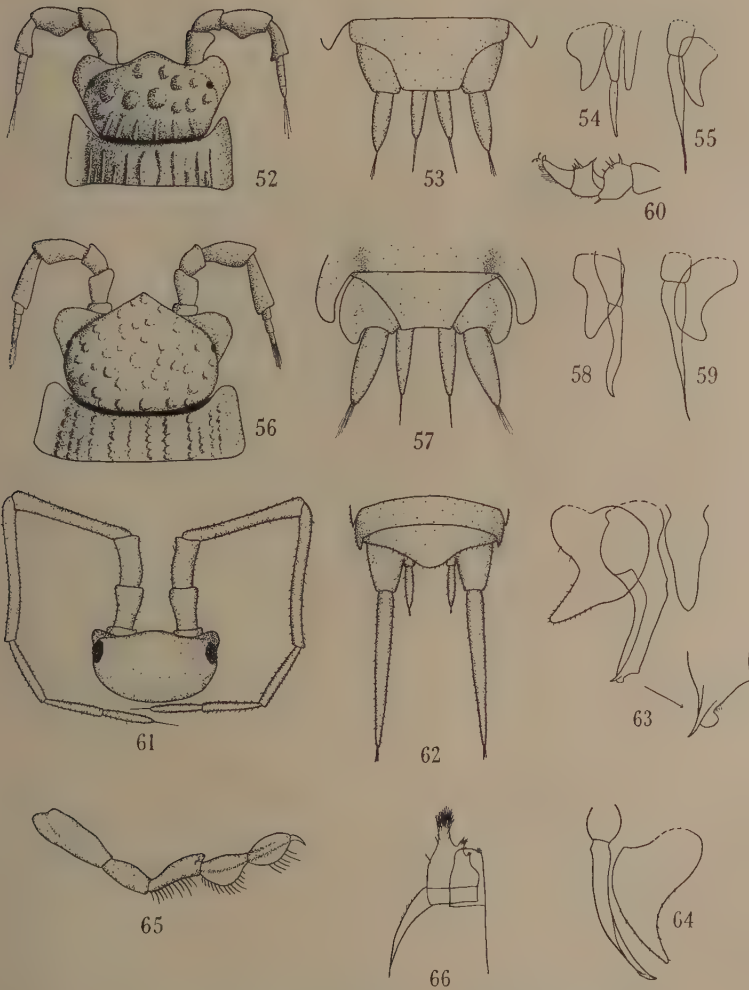
Characters.

Small to large animals in which the eyes are compound (except in *Platyarthrus* where they are absent) and which do not possess pseudotracheae. Epimera more or less well developed, either expanded laterally or adpressed. The number of flagellar segments is always three or less, and they are distinct. Legs often very long and spinose; rami of the uropods visible from above, the exopodites differing to a greater or less extent from the endopodites.

Genus **PHILOSCIA** Latreille, 1804.

Characters.

General shape rather oval, the epimera well developed, even on the pleon, projecting ventro-laterally from the body. Integument smooth, lateral lobes of the head absent, antennae not strikingly hairy (fig. 67). Endopodites of the maxillipeds without a ciliated apical border (fig. 71). 1st to 3rd pereopods of males with a brush of bristles on the mero- and carpopodites, the propodite not expanded. Endopodite of the 1st male pleopod narrowing gradually apically, the apex itself rounded (fig. 69).



FIGS. 52-55.—*Haplophthalmus menzei* (Zaddach). 52, head and 1st pereopod, $\times 28$; 53, telson and uropods, $\times 28$; 54, 1st δ pleopod and penis, $\times 40$; 55, 2nd δ pleopod, $\times 40$.

FIGS. 56-60.—*Haplophthalmus danicus* Budde-Lund. 56, head and 1st pereopod, $\times 28$; 57, telson and uropods, $\times 28$; 58, 1st δ pleopod and penis, $\times 40$; 59, 2nd δ pleopod, $\times 40$; 60, 7th δ pereopod, $\times 20$.

FIGS. 61-66.—*Halophiloscia couchii* (Kinahan). 61, head, $\times 13$; 62, telson and uropods, $\times 13$; 63, 1st δ pleopod and penis, $\times 16$; 64, 2nd δ pleopod, $\times 16$; 65, 1st δ pleopod, $\times 16$; 66, apical part of maxilliped, $\times 68$.

Philoscia muscorum (Scopoli). (Figs. 67-71.)*Oniscus muscorum* Scopoli, 1763.*Oniscus sylvestris* Fabricius, 1793.*Oniscus agilis* Koch, in Panzer, 1793.*Philoscia marmorata* Brandt, 1833.*Ligia melanocephala* Koch, 1837.*Zia melanocephala* Koch, 1847.*Characters.*

Up to 10.0 mm. long, only twice as long as wide or slightly longer, general outline oval, but the base of the pleon distinctly narrower than the pereion. Integument smooth and glabrous. Colour various, often a light or dark brown, with darker to black mottled markings, the latter with a tendency to longitudinal arrangement, particularly near the lateral borders of the tergites. Antennae long, for the most part glabrous, with a small number of inconspicuous bristles; last peduncular segment seven to eight times as long as wide; flagellum of three distinct segments, together longer than the last peduncular segment, the proximal segment up to one-third longer than either of the other two. Head smooth, 1.8 times as wide as long, without lateral lobes, but with a distinct frontal carina marking the anterior margin of the upper surface. Epimera well developed, those of the pereion not expanded laterally, and not very strongly produced posteriorly, those of the pleon becoming laterally flattened and more strongly produced posteriorly, their apices acuminate. Telson triangular, strongly angulate in the middle. Exopodites of the uropods twice wider at the base than the endopodites and four times as long as wide, somewhat flattened dorsoventrally. 1st to 3rd pereiopods of males with a distinct brush of bristles on the lower margin of the carpopodite; the propodites not expanded. Endopodite of the maxillipeds non-ciliated but with two stout spines; the inner spine wider and apparently truncate.

Distribution.

Widespread, from all parts of the British Isles, usually in moist situations, rubbish heaps, under the carpet of dead leaves in woods, etc.

Genus *HALOPHILOSCIA* Verhoeff, 1908.

This genus was established by Verhoeff as one of the several genera into which he divided the old group *Philoscia* of Scopoli. It is quite clearly distinct from *Philoscia* s. s. and is represented in Britain by the type species, *couchii* Kinahan.

Characters.

Integument sparsely spinose, the antennae more strongly so. Head with lateral lobes, its anterior margin acarinate (fig. 61). Endopodites of the maxillipeds ciliated, with a small tubercle near the inner edge bearing a short brush, exopodite with a strong terminal brush and two smaller brushes on the inner margin (fig. 66). Epimera as in *Philoscia* but those of the pleon not so strongly developed. 1st to 3rd pereiopods of males with the mero- and propodites strongly expanded, the former below, the latter above and below (fig. 65). Endopodites of the 1st male pleopods broad for the whole of their length, with a strong postero-laterally directed spine at the apex (fig. 63). Base of the pleon distinctly narrower than the pereion.

Halophiloscia couchii (Kinahan), 1857. (Figs. 61-66.)*Ligidium couchii* Budde-Lund, 1885.*Halophiloscia venata* Santucci, 1930.*H. adriatica rupium* Verhoeff, 1931.

Characters.

Up to 10.0 mm. long, two and a half times as long as wide. Colour, grey. Antennae very long, strongly spinose, the last peduncular segment ten times as long as wide; flagellum longer than the last peduncular segment, its own proximal segment up to half as long again as either of the other two. Head about twice as wide as long, with distinct though feeble lateral lobes, its upper surface together with that of the trunk sparsely spinose, particularly near the margins of the sclerites, the lateral margins themselves distinctly spinose. Epimera of the pereon round behind, those of the pleon sharply pointed. Telson only feebly produced behind and broadly rounded. Exopodites of the uropods nearly five times as long as the endopodites and ten times as long as wide at the base. Carpo- and propodites of the first three male pereopods characteristically enlarged, and together with the meropodite, bearing a fringe of hairs on the lower margins.

Distribution.

Widely distributed round the coasts of the British Isles as well as the Atlantic and Mediterranean coasts of Europe.

Genus CHAETOPHILOSCIA Verhoeff, 1908.

This genus, like the preceding, was established by Verhoeff when he reclassified the old *Philoscia* group. The species *Philoscia patiencei* Bagnall is something of an enigma: one of the main distinctions between Verhoeff's Tribes *Halophilosciini* to which *Halophiloscia* belongs, and *Onisciini* to which *Philoscia* s. str. and *Chaetophiloscia* among others belong, is that members of the former have a ciliated apical border to the endopodite of the maxilliped. Now *patencei*, although clearly distinct from *Halophiloscia* and resembling *Chaetophiloscia* in many other characters, does have the ciliated apical margin referred to. In view of the fact that the male genitalia are quite unlike *Halophiloscia*, I propose to include the species for the present in the genus *Chaetophiloscia* to which it bears resemblances in other ways.

Characters.

Integument sparsely spinose, antennae much shorter than in the other genera, not conspicuously hairy as in *Halophiloscia* but with a number of short relatively stout spines and fine, short bristles. Head without lateral lobes, and without the transverse frontal carina. Exopodite of the maxillipeds with a strong terminal brush but without the two lateral brushes (fig. 75). Epimera not so well developed as in the other genera, those of the pleon very feeble. Pereiopods of males not expanded, and without brushes. Telson not strongly produced, rounded behind. Pleon distinctly narrower than the pereon. Endopodites of the 1st male pleopods narrowing apically from about half their length, without an apico-lateral tooth as in *Halophiloscia*.

Chaetophiloscia patiencei (Bagnall), 1908. (Figs. 72-77.)

Philoscia patiencei Bagnall, 1908 a.

Characters.

This is a much smaller species than either *P. muscorum* or *H. couchii*, only 3.0 mm. long, and two and a half times as long as wide. Colour in life "more or less violaceous brown, marbled with white, and with a broken white median band along the back of the mesosome" (Bagnall). Dorsal surface without tubercles, with a few irregularly distributed fine hairs. Antennae short, last peduncular segment a little more than three times as long as wide; flagellum of two segments, terminating in a single stout spine (Bagnall, figures three segments, but I have examined the type material and only two

are present), the 1st segment two-thirds as long as the 2nd and a little longer than wide. Head one and a half times as wide as long, without distinct lateral lobes and without a frontal carina. Pleon epimera poorly developed, not expanded laterally. Endopodite of the maxillipeds finely ciliated along the apical margin (see comments under generic description). Telson broadly rounded behind, not produced in the middle. Exopodites of the uropods conical, three times as long as wide, endopodites half as long as the exopodites, rather compressed in shape, ciliated along the inner margin. Male pereopods not differing from those of the female. Penis and 1st and 2nd male pleopods represented in figs. 73 and 74.

Distribution.

Originally described from Kew Gardens; Bagnall considered material from a garden at Winlanton, Durham, to be conspecific. Subsequent records from Cheshire and Lancashire are rather doubtful, some of this material is certainly not *patiencei*, but another species of *Chaetophiloscia*; there is at present however, insufficient material upon which to base a description of a new species.

Genus PLATYARTHURUS Brandt, 1833.

Typhloniscus Schobl, 1860.

Characters.

Colourless and without eyes, integument finely, irregularly or regularly tuberculate. General outline oval, with no discontinuity between pereion and pleon; the epimera of both strongly developed and expanded laterally, those of the pleon strongly produced backwards, their apices acuminate. Antennae very short and spinose, their flagella with two segments, the 1st very short (fig. 78). Pleopods without tracheae. Inner and outer rami of the uropods very different in shape (fig. 79).

Platyarthrus hoffmannseggii Brandt, 1833. (Figs. 78-81.)

Ilea crassicornis Koch, 1844.

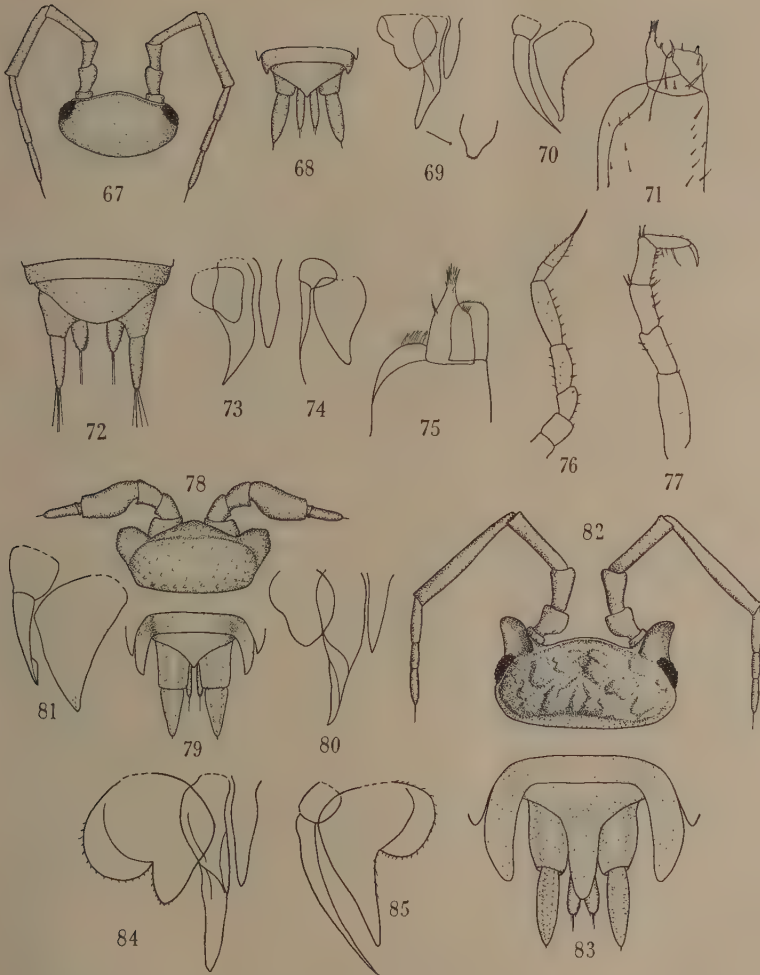
Typhloniscus steinii Schobl, 1860.

Characters.

Up to 3.6 mm. long, distinctly oval in outline, less than twice as long as wide. Colour white. Antennae short and stout, the whole surface covered with minute scale-like spines; last peduncular segment longer than any other, itself twice as long as wide; flagellum of two segments, the 1st extremely small, the 2nd conical, nearly as long as the last peduncular segment, but less than half as wide as the latter. Head with very strong lateral lobes, including these it is twice as wide as long; the upper surface, together with that of the rest of the body, minutely and irregularly tuberculate. Eyes absent. Epimera very well developed, their margins minutely denticulate on both pereion and pleon, those on the pleon very strongly produced backwards, their apices acuminate. The whole dorsal surface of the animal much less strongly convex than in *Philoscia* sensu lato. Telson produced in the middle to a sharp point. Exopodites of the uropods short and stout, up to twice as long as wide, strongly depressed, lanceolate; the endopodites much less readily visible, their bases hidden by the telson; as long as the outer pair but only a quarter as wide. 1st and 2nd male pleopods as in figs. 80 and 81.

Distribution.

This species occurs throughout Great Britain and Ireland (and the rest of Europe) in the nests of ants.



FIGS. 67-71.—*Philoscia muscorum* (Scopoli). 67, head, $\times 13$; 68, telson and uropods, $\times 13$; 69, 1st δ pleopod and penis, $\times 16$; 70, 2nd δ pleopod, $\times 16$; 71, apical part of maxilliped, $\times 68$.

FIGS. 72-78.—*Chaetophiloscia patiencei* (Bagnall). 72, telson and uropods, $\times 28$; 73, 1st δ pleopod and penis, $\times 28$; 74, 2nd δ pleopod, $\times 28$; 75, apical part of maxilliped, $\times 110$; 76, antenna, $\times 52$; 77, 1st δ pereopod, $\times 52$.

FIGS. 78-81.—*Platyarthrus hoffmannseggii* Brandt. 78, head, $\times 28$; 79, telson and uropods, $\times 28$; 80, 1st δ pleopod and penis, $\times 68$; 81, 2nd δ pleopod, $\times 68$.

FIGS. 82-85.—*Oniscus asellus* Linné. 82, head, $\times 13$; 83, telson and uropods, $\times 13$; 84, 1st δ pleopod and penis, $\times 20$; 85, 2nd δ pleopod, $\times 20$.

Genus *ONISCUS* Linné, 1767.*Characters.*

Integument without hairs or tubercles but thrown into a number of irregular, low undulations. Body moderately convex above, the epimera very strong, those of the last three segments of the pleon produced outwards and backwards, the last pair reaching back farther than the base of the exopodites of the uropods; the latter visible from above but of different shape from the endopodites (fig. 83). Telson strongly produced backwards. Antennae moderately long, their flagella of three distinct segments, the 2nd peduncular segment with a strong inward incrustation (fig. 82). Eyes compound, lateral lobes of the head strong. Maxillipeds without a ciliated apical border to the endopodite but with two stout spines, the exopodite also with two stout spines on the inner margin. Pleopods without pseudotracheae. Exopodite of the 1st and 2nd male pleopods with a strong emargination on the latero-posterior margin, endopodite of the 2nd pair two-jointed, the distal joint drawn out to a long fine style (figs. 84 and 85.)

Oniscus asellus Linné, 1767.

Oniscus fossor Koch, 1838; Bate & Westwood, 1868.

Characters.

This is one of our largest and commonest woodlice. Up to 15 mm. long, about twice as long as wide. Colour various, usually slaty grey with irregular lighter markings. Antennae with only an extremely fine pile of hairs, the last segment of the peduncle longer than the rest and about seven times as long as wide, the flagellum rather shorter than the last peduncular segment, composed of three segments, the middle one often the shortest. Lateral lobes of the head very strong, their upper surface concave. The head twice as wide (without the lateral lobes) as long, strongly carinate along the anterior margin which is broadly rounded in front. Epimera of the 1st pereonite produced forwards round the sides of the head, the posterior margins of the 1st three epimera broadly emarginate, those of the other somites not curving forwards before they turn posteriorly. Telson triangular, with a very strong median process, the sides nearly twice as long as the distance across the base, the apex rounded. Exopodites of the uropods depressed, lanceolate, their apices rounded, about two and a half times as long as wide. The endopodites much narrower, nearly tubular, their bases concealed (from above) by the telson.

Distribution.

Ubiquitous in the British Isles.

Family **Porcellionidae** Verhoeff, 1917b.*Characters.*

Large animals with compound eyes and pseudotracheae. Epimera very well developed and often expanded laterally and posteriorly. Flagellum always with two distinct segments, head often with well-developed lateral and frontal lobes. Rami of the uropods usually visible from above, though the endopodites may be nearly totally concealed by the telson, which is often strongly produced (figs. 87, 91, etc.); the exopodites very different in shape from the endopodites. Animals adapted to live in drier conditions than the Oniscidae or Trichoniscidae.

Genus CYLISTICUS Schnitzler, 1853.

Characters.

Integument glabrous, minutely granular. Eyes compound, antennae with two flagellar segments. Dorsum of body strongly convex, capable of rolling into a ball; the epimera well developed but not expanded laterally; no break in the outline between pereion and pleon. Telson strongly produced posteriorly, nearly covering the endopodites of the uropods, which are much smaller and narrower than the exopodites (fig. 87). The exopodites of all five pairs of pleopods possess pseudotracheae. Endopodites of the 1st male pleopods wide at the base and becoming suddenly much narrower half way along; the narrower portions somewhat divergent from the median line, 2nd endopodites styliform (figs. 88 and 89).

One British species.

Cylisticus convexus (De Geer). (Figs. 86-89.)

Oniscus convexus De Geer, 1778.

Porcellio spinifrons Brandt, 1833.

P. laevis Koch, 1836; *nec* Latreille, 1804.

P. armadilloides Lereboullet, 1853; Bate & Westwood, 1868.

Cylisticus laevis Schnitzler, 1853.

Characters.

Up to 15 mm. long, 2.2 times as long as wide. Slaty grey in colour, with irregular light markings, the exopodites of the uropods (which are visible from above) ferruginous. Antennae long and very finely spinose, the last peduncular segment nine times as long as wide, longer than the flagellum, which is composed of two equal joints. Head strongly transverse, two and a half times as wide as long, the lateral lobes well developed, the frontal lobe small and pointed. Body strongly convex both transversely and longitudinally; the epimera not expanded laterally, those of the 1st pleonite strongly produced forwards and backwards, reaching the lateral lobes of the head in front; those of the last segment of the pleon very strongly produced backwards, their apices curving inwards. Median process of the telson twice as long as wide at the base, tapering apically to a rounded point. Exopodites of the uropods depressed lanceolate, three times as long as wide at the base; the endopodites much narrower, compressed laterally, their apices reaching just beyond the tip of the telson.

Distribution.

The species is recorded from most counties of England and Scotland, from Glamorgan in Wales and from several districts in Northern Ireland and Eire. In the writer's experience it is associated with calcareous soils.

Genus METOPONORTHUS Budde-Lund, 1879.

Porcellionides Miers, 1877, in part.

Vandel, in his review of the genus (1946 b), points out that the name *Porcellionides* of Miers, though earlier, does not refer to the group of species which are now considered to form this genus, but to a much larger group including several subgenera of *Porcellio*. *Metaponorthus* as defined by Budde-Lund is separated from *Porcellio* mainly on the grounds that the base of the pleon is narrower than the pereion, a character which excludes a large part of Miers' genus,

Characters.

Head with a well-developed frontal carina, but feeble lateral lobes and no frontal lobe (fig. 90). Integument smooth or feebly tuberculate, usually covered with a fine 'bloom'. The antennae minutely spinose. A transverse impression sometimes present on the tergites of the pereion. Pleon narrower than the pereion, the epimera poorly developed in comparison with *Porcellio*. Telson triangular, never produced into a long point (fig. 91). General form of the body moderately convex, the sides more or less parallel. Antennae fairly long, the flagellum of two segments. Endopodite of the maxillipeds with two spines on the apical margin and a longer one originating below the margin. The exopodites of the 1st two pleopods bearing pseudotracheae. Exopodite of the 1st male pleopods rounded behind, those of the 2nd pair produced posteriorly; the 1st endopodites more or less narrowed apically, those of the 2nd styliiform (figs. 92 and 93).

Key to the species of Metoponorthus.

- | | |
|--|------------------------------|
| 1. Tergites of the pereion with a distinct transverse carina in the anterior half | <i>cingendus</i> (Kinahan). |
| — Tergites without such a carina | 2. |
| 2. Last peduncular segment of the antenna six times as long as wide, proximal segment of the flagellum longer than the distal, head gently rounded in front, lateral lobes present (fig. 94) | <i>pruinus</i> (Brandt). |
| — Last peduncular segment four times as long as wide, flagellar segments equal in length, head with a stronger anterior lobe, lateral lobes feebler to absent (fig. 98) | <i>melanurus</i> Budde-Lund. |

Metoponorthus cingendus (Kinahan). (Figs. 90–93.)

Porcellio cingendus Kinahan, 1857; Bate & Westwood, 1868.

Metoponorthus simplex Budde-Lund, 1885.

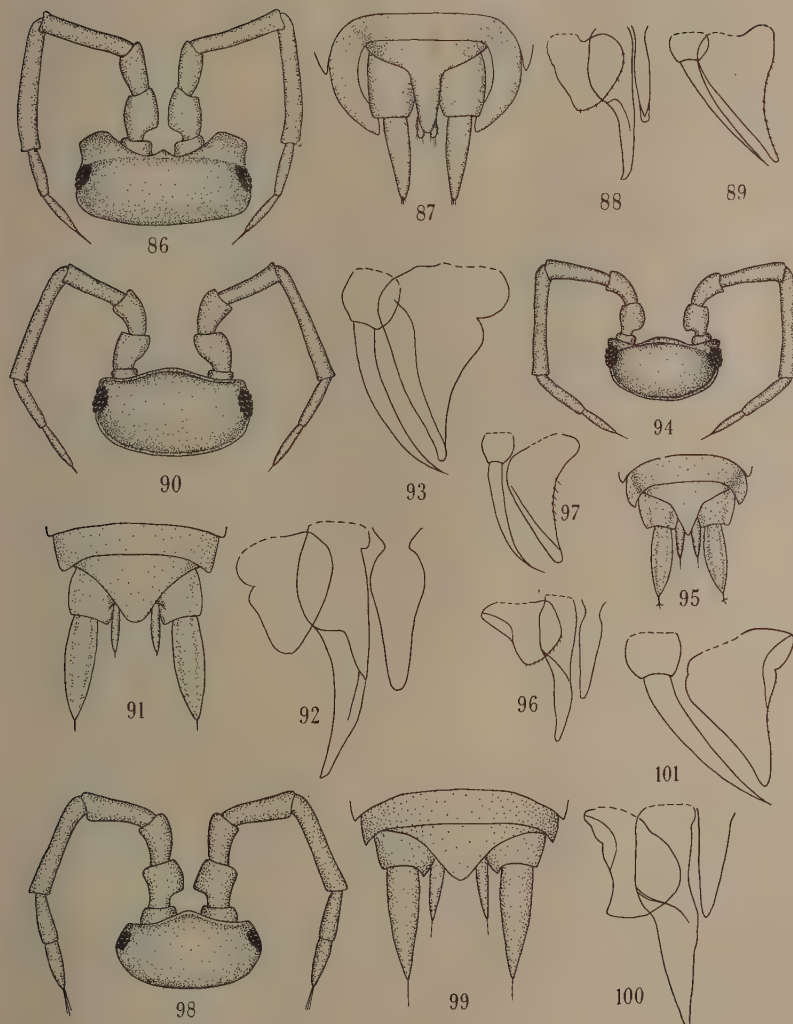
M. lusitanorum Arcangeli, 1935.

Characters.

Up to 7.0 mm. long, two and a half times as long as wide, rather oval in outline. Colour very variable, from black through brown to red, marbled with irregular patches, often with a median light streak. Antennae long, covered with minute hair-like scales, the last peduncular segment seven to eight times as long as wide, equal to or rather longer than the flagellum, whose proximal segment is a little longer than the distal. Head one and a half times as wide as long, the anterior margin carinate and feebly convex in front, lateral lobes virtually absent. Dorsum of the head and trunk with a number of low irregular elevations, each tergite of the pereion with a fine but distinct transverse carina in the anterior half. Telson triangular, the apex rounded, the sides convex. Exopodites of the uropods very much larger than the endopodites, somewhat depressed, lanceolate, and about four times as long as wide; the endopodites rather less than half as long and only a fifth as wide when seen in dorsal view—they are, however, strongly compressed laterally. The male genitalia differ from those of *pruinus* as follows: both the 1st and 2nd exopodites bear a narrow V-shaped emargination on their outer margins and they are without bristles; also the tip of the 2nd is recurved medially (cf. figs. 92, 93 and 96, 97).

Distribution.

The species is recorded from nearly all the coastal counties of Eire (but not of Northern Ireland) and from Devon and the Isle of Wight. It also occurs on the Atlantic coast of France, Spain and Portugal,



FIGS. 86-89.—*Cylisticus convexus* (De Geer). 86, head, $\times 13$; 87, telson and uropods, $\times 13$; 88, 1st σ pleopod and penis, $\times 13$; 89, 2nd σ pleopod, $\times 13$.
 FIGS. 90-93.—*Metoponorthus cingendus* (Kinahan). 90, head, $\times 13$; 91, telson and uropods, $\times 13$; 92, 1st σ pleopod and penis, $\times 20$; 93, 2nd σ pleopod, $\times 20$.
 FIGS. 94-97.—*Metoponorthus pruinosis* (Brandt). 94, head, $\times 13$; 95, telson and uropods, $\times 13$; 96, 1st σ pleopod and penis, $\times 16$; 97, 2nd σ pleopod, $\times 16$.
 FIGS. 98-101.—*Metoponorthus melanurus* Budde-Lund. 98, head, $\times 13$; 99, telson and uropods, $\times 28$; 100, 1st σ pleopod and penis, $\times 28$; 101, 2nd σ pleopod, $\times 28$.

Metoponorthus pruinosus (Brandt), 1833. (Figs. 94-97.)*Porcellio pruinosus* Brandt, 1833; Bate & Westwood, 1868.*P. truncatus* Milne-Edwards, 1840.*P. maculicornis* Koch, 1840.*P. frontalis* Lereboullet, 1853.*Porcellionides flavo-vittatus* Miers, 1877.*Characters.*

Up to 9.0 mm. long, a little more than twice as long as wide. Colour in life, bluish grey, becoming dark reddish brown if the bloom is rubbed off. Antennae moderately long, covered with minute spine-like scales, the last peduncular segment six times as long as wide and equal to the length of the flagellum, which is composed of two segments, the proximal segment one and a half times as long as the distal. Head and dorsum of the pleon and pereion covered with minute scales forming the bloom, the surface thrown into a number of low, irregularly shaped elevations, with a tendency to transverse arrangement. The tergites quite without a transverse impression or carina. The head with a well-developed transverse carina in front, continuous laterally with the margin of the rather feeble lateral lobes. Frontal margin distinctly but not strongly bi-sinuate. Epimera not so strong as in *Porcellio*, those of the pereion not produced backwards or expanded laterally, those of the pleon rather feebly so. Telson triangularly produced in the middle, the apex sharp. Exopodites of the uropods lanceolate, three and a half times as long as their greatest width, which is near the base; endopodites only half as long and one-fifth as wide as the exopodites, conical rather than lanceolate.

Distribution.

Widely distributed throughout the British Isles, though not one of the most common species.

Metoponorthus melanurus Budde-Lund, 1885. (Figs. 98-101.)*Characters.*

Up to 6.0 mm. long, more than two and a half times as long as wide (longer and narrower in proportion to *pruinosus*). Colour in life unknown to me; judging by the figure published by Beresford & Foster (1911) this would be dark, with a number of lighter longitudinal markings and a similar median streak. Antennae covered with minute scales, the last peduncular segment a little over four times as long as wide, slightly longer than the flagellum, the segments of which are approximately equal in length. Anterior margin of the head strongly carinate, produced in the middle to a blunt point, the lateral lobes virtually absent. Dorsal surface of the animal bearing minute scales, otherwise smooth, not showing the distinct elevations of *pruinosus* or the transverse impressions of *cingendus*. Telson triangularly produced in the middle, its apex rounded. The uropods do not differ significantly from those of *pruinosus*. Male genitalia differ from those of *pruinosus* mainly in the shape of the 1st exopodite which is angulate between the posterior and lateral margins in *melanurus*, rounded in *pruinosus* (figs. 100 and 101).

Distribution.

Recorded only from Dublin County (under grass on Howth Cliffs). It is also known to occur in Southern France, Corsica and other Mediterranean coasts. In this respect it rather resembles *Oritoniscus flavus*, known only from the Pyrenees, Corsica and Ireland,

Genus PORCELLIO (Latreille, 1804), Budde-Lund, 1908.

This genus has from time to time been split into several subgenera. So far as the British species are concerned, Budde-Lund placed *laevis* in his subgenus *Gymnoderma*, and the species *ratzeburgi* and *rathkei* in his subgenus *Trachelipus*. Neither of these subgenera was adequately defined. *Gymnoderma* is no longer recognized by most workers (see Vandel, 1951), so that *laevis* can well remain in *Porcellio* sensu stricto. There is a better case, however, for distinguishing *rathkei* and *ratzeburgi* from other species, since they both have pseudotracheae on all five pairs of pleopods.

Verhoeff (1917 b) established the subgenus *Tracheoniscus* to receive those species with five pairs of pseudotracheae which are little branched and which he says open by a row of pores along the external margin of the pleopod (instead of the single opening from a richly branched organ characteristic of other species). This subgenus is well defined and is to be preferred to Budde-Lund's *Trachelipus*.

Now Vandel (1946 b) has proposed a sub-division on the family Porcellionidae into two main subfamilies (besides other minor ones) which he designates '*Porcellionidae bitracheatae*' and '*Porcellionidae quinquetracheatae*'. This system entails grouping Verhoeff's subgenus *Tracheoniscus* (which Vandel considers as a genus) in the second of these subfamilies, while the genus *Metoponorthus* of Budde-Lund belongs to the first. Such a division implies that the two species *Tracheoniscus rathkei* and *T. ratzeburgi* are less closely related to the rest of the genus *Porcellio* than the species of *Metoponorthus* are; an implication which, in the present writer's view, is unfortunate, particularly in view of the fact that there are species of *Porcellio* which show an intermediate number of pseudotracheae, and that, as Collinge (1942) has shown, occasional specimens of most species of *Porcellio* (and of other genera), including *Metoponorthus* and *Cylisticus* have abnormal numbers of pseudotracheae. Furthermore, Herold (1925) finds Verhoeff's description of the pseudotracheae of *rathkei* and *ratzeburgi* faulty; they do not open by several pores, but by one.

For the present, therefore, *Tracheoniscus* will be recognized as a subgenus of *Porcellio*, including the two British species *rathkei* and *ratzeburgi*.

Characters.

Large animals, not capable of rolling into a ball. Integument smooth or tuberculate. Head with well-developed frontal and lateral lobes (e.g. figs. 106 and 110). Antennae with very small hair-like scales, but without spines, the flagellum always with two segments. Epimera very well developed, produced backwards (and forwards from the 1st pereonite). Telson strongly produced in the middle (figs. 103, 107, etc.). Endopodites and exopodites of the uropods very different in shape, the former often more or less concealed from above. At least the 1st two pleopodal exopodites with pseudotracheae. Apical margin of the endopodite of the maxilliped with three short spines. Exopodites of the 2nd male pleopods elongated posteriorly, those of the 1st pair variously shaped, often with emarginations.

Key to the species of Porcellio.

- | | |
|---|--------------------------|
| 1. Pseudotracheae on two pairs of pleopods only (subgenus <i>Porcellio</i> Verhoeff) | 2. |
| — Pseudotracheae on more than two pairs of pleopods (subgenus <i>Tracheoniscus</i> Verhoeff) | 5. |
| 2. Head and body smooth | <i>laevis</i> Latreille. |
| — At least the head tuberculate | 3. |
| 3. Frontal lobe of the head evenly rounded, the junction of its margin with those of the lateral lobes forming sharp, V-shaped incisions (fig. 110) | <i>spiniornis</i> Say. |
| — Frontal lobe of the head triangular—the apex rounded but the sides straight | 4. |

- 4 Median process of the telson parallel sided (fig. 107), animals not more than 1.7 times as long as wide *dilatatus* Brandt.
 -. The sides of the median process of the telson divergent towards the base; animals nearly or quite twice as long as wide *scaber* Latreille.
 5. Distal flagellar segment about one-third longer than the proximal, anterior margin of the head (as seen from above) smoothly, concave between the frontal and lateral lobes (fig. 118). *rathkei* (Brandt).
 -. Distal flagellar segment twice as long as the proximal, anterior margin of the head with a sharp, V-shaped incision between the lateral and frontal lobes (fig. 122) *ratzeburgi* (Brandt).

Porcellio (Porcellio) laevis Latreille, 1804. (Figs. 102-105.)

Cylisticus laevis Schnitzler, 1853.

Gymnoderma laevis Budde-Lund, 1909.

Characters.

A very large species, up to 18 mm. long, females about 1.7 times, and males 2.1 times as long as wide—these however are only mean values, the variation is considerable. Colour usually light grey with irregular white markings. Antennae long, the last peduncular segment seven times as long as wide at the apex and about one-sixth as long again as the flagellum. Dorsal surface of the animal quite without tubercles, minutely granular. Frontal lobes of the head gently rounded, not very strong, the lateral lobes strong, rounded apically, their upper surfaces concave. Telson produced in the middle rather more strongly than in *scaber*, the sides strongly excavate, the apex rounded, the upper surface distinctly concave. Exopodites of the uropods distinctly longer in proportion to their width than in *scaber*, nearly four and a half times as long as wide, strongly depressed; the endopodites about half as long as the exopodites, and nearly six times as long as wide; the endopodites, however, reaching well beyond the tip of the telson. Pseudotracheae on the 1st two pairs of pleopods. 1st and 2nd male pleopods as in figs. 104 and 105.

Distribution.

The species is recorded from several English counties from the Channel Isles to Cumberland; from Dumbarton in Scotland, from Flint in Wales, and from several coastal counties in Ireland.

Porcellio (Porcellio) spinicornis Say, 1818. (Figs. 110-113.)

Porcellio pictus Brandt, 1833.

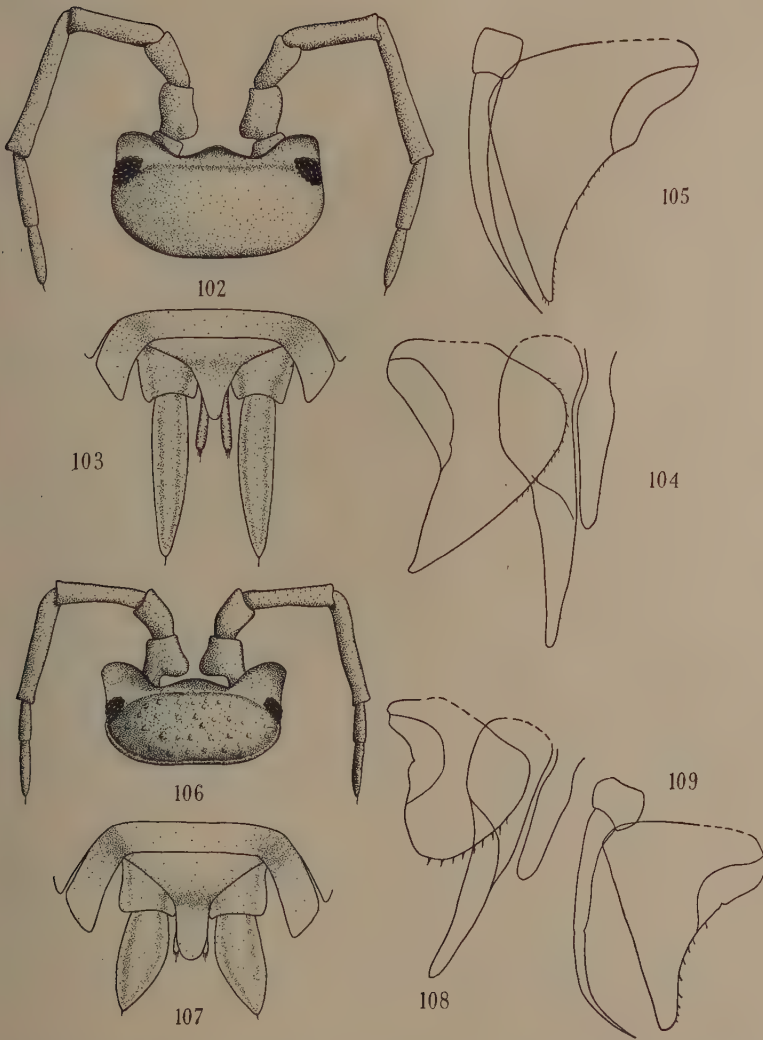
P. melanocephalus Koch, 1841.

P. mixtus Fitch, 1856.

P. germanicus Verhoeff, 1896.

Characters.

Length up to 12 mm., about twice as long as wide. Head black, the pereon and pleon dark brown with yellowish markings, the former usually with a black median strip, the epimera often lighter, the pleon sometimes almost black. Antennae minutely scaled, the last peduncular segment six times as long as wide and one-fifth as long again as the flagellum, whose proximal segment is slightly longer than the distal. Head coarsely tuberculate above, the tubercles in irregular transverse rows; anterior margin of the frontal lobe continuously rounded over the whole of its length, lateral lobes not reaching so far anteriorly as in *dilatatus*, their lateral margins not continuously rounded but very broadly angled in the middle. The rest of the dorsum of the animal rather feebly tuberculate, the tubercles not restricted to the middle of the segments as in *dilatatus*. Telson triangularly produced in the middle. Pseudotracheae on the 1st two pairs of pleopods. Exopodites



FIGS. 102-104.—*Porcellio (Porcellio) laevis* Latreille. 102, head, $\times 13$; 103, telson and uropods, $\times 13$; 104, 1st δ pleopod and penis, $\times 20$; 105, 2nd δ pleopod, $\times 20$.
 FIGS. 106-109.—*Porcellio (Porcellio) dilatatus* Brandt. 106, head, $\times 13$; 107, telson and uropods, $\times 13$; 108, 1st δ pleopod and penis, $\times 20$; 109, 2nd δ pleopod, $\times 20$.

of the uropods two and a half times as long as wide, strongly depressed, lanceolate; the endopodites somewhat compressed laterally, three-quarters as long as the exopodites, five times as long as wide, their tips reaching beyond the apex of the telson.

Distribution.

Very widely distributed throughout the British Isles.

Porcellio (Porcellio) dilatatus Brandt, 1833. (Figs. 106-109.)

Porcellio scaber Milne-Edwards, 1840, *nec* Latreille, 1804.

Characters.

Length up to 15 mm., rather less than twice as long as wide, and more oval shaped than *scaber*. Colour, a rather lighter grey than in *scaber*. Antennae moderately long, minutely spinulose, the last peduncular segment five and a half times as long as wide and one-fifth as long again as the flagellum; the two segments of the latter approximately equal in length, the proximal segment nearly four times as long as wide. Head nearly twice as wide as long, its dorsal surface bearing tubercles arranged in more or less regular transverse rows. Frontal lobe projecting upwards at an angle to the plane of the head in the form of a very low triangle, the apex rounded but the sides straight. Lateral lobes strong, their margins not so smoothly rounded as in *scaber*, broadly angulate at the antero-lateral corners. Tergites of the pereon each with a transverse area in the middle which is coarsely tuberculate, the tubercles less distinct on the pleonites except for the posterior margin of each, which is feebly crenulate. Pseudotracheae on the first two pairs of pleopods only. Epimera strong, those of the pleon expanded in a lateral plane, those of the anterior segments of the animal continuous with the general convex surface of the dorsum (but no sharp change in shape between the two extremes). Telson strongly produced posteriorly, the sides of the process parallel (except at the apex which is gently rounded), and different in this respect from all other British species. Exopodites of the uropods very wide, two and a half times as long as wide, strongly depressed, lanceolate; the endopodites not reaching the tip of the telson, not much shorter than the exopodites, but cylindrical and five times as long as wide. 1st and 2nd male pleopods as in figs. 108 and 109.

Distribution.

The species is recorded from most counties in England and Scotland, and from several in Northern and Southern Ireland.

Porcellio (Porcellio) scaber Latreille, 1804. (Figs. 114-117.)

Oniscus granulatus Lamarck, 1818.

Porcellio nigra Say, 1818.

P. brandtii Milne-Edwards, 1840.

P. dubius Koch, 1840.

P. asper Koch, 1847.

P. montezumae Saussure, 1857.

P. paulensis Heller, 1865.

P. graniger Miers, 1876, Budde-Lund, 1885.

Characters.

Up to 17.0 mm. long and nearly twice as long as wide. Very variable in colour, usually dark slaty grey with irregular, lighter markings, but varying from pink to black, the epimera often lighter than the dorsum of the body. Antennae minutely scaled, the last peduncular segment about six times as

long as wide and one-fourth or less as long again as the flagellum, the 2nd segment of the latter about the same length as the 1st. Dorsum of the head and trunk strongly, irregularly tuberculate (the tubercles on the head however forming more or less regular transverse rows); on the posterior segments, and particularly on the pleon, the tubercles sometimes forming crenulations at the posterior margins of the tergites. Frontal lobe of the head triangular, the lateral lobes strong, rounded apically, their upper surfaces concave. Telson strongly produced behind, rather variable in shape, the sides excavate, the apex more or less rounded. Exopodites of the uropods about two and a half times as long as wide, strongly depressed; the endopodites shorter than the exopodites and five times as long as wide, nearly tubular. The 1st two pairs of pleopods with pseudotracheae. 1st and 2nd male pleopods as in figs. 116 and 117.

Distribution.

This is the commonest species of *Porcellio*, and, with *Oniscus*, the commonest British woodlouse. It is recorded from all over the British Isles.

Subgenus *TRACHEONISCUS* Verhoeff, 1917 b.

Porcellio (*Tracheoniscus*) *rathkei* (Brandt), 1833. (Figs. 118-121.)

P. ferrugineus Brandt, 1833.

P. trilineatus Koch, 1840.

P. trivittatus Lereboullet, 1853.

P. tetramoerus Schnitzler, 1853.

P. striatus Schnitzler, 1853.

Trachelipus rathkei Budde-Lund, 1909.

Characters.

Up to 15 mm. long, two and a quarter times as long as wide. Colour, dark greyish brown with lighter markings particularly on the middle of the tergites and on the epimera. Antennae minutely scaled, the last peduncular segment nearly seven times as long as wide, and about one-seventh as long again as the flagellum, the distal segment of the latter one-third as long again as the proximal. Head rather shallowly and irregularly tuberculate, the apical margin of the frontal lobe continuously rounded, lateral lobes also rounded; neither lobe as strong as in most other species of the genus. Dorsum of the body irregularly and shallowly sculptured rather than tuberculate, but often almost smooth. Pseudotracheae on all five pairs of pleopods, the tubes feebly branched. Telson triangularly produced in the middle, the apex narrowly rounded. Exopodites of the uropods nearly three times as long as wide, depressed and lanceolate; endopodites about three-quarters as long as the exopodites, bearing a number of long bristles, somewhat compressed laterally. 1st and 2nd male pleopods as in figs. 120 and 121.

Distribution.

Very widely distributed throughout the British Isles.

Porcellio (*Tracheoniscus*) *ratzeburgi* (Brandt), 1833. (Figs. 122-125.)

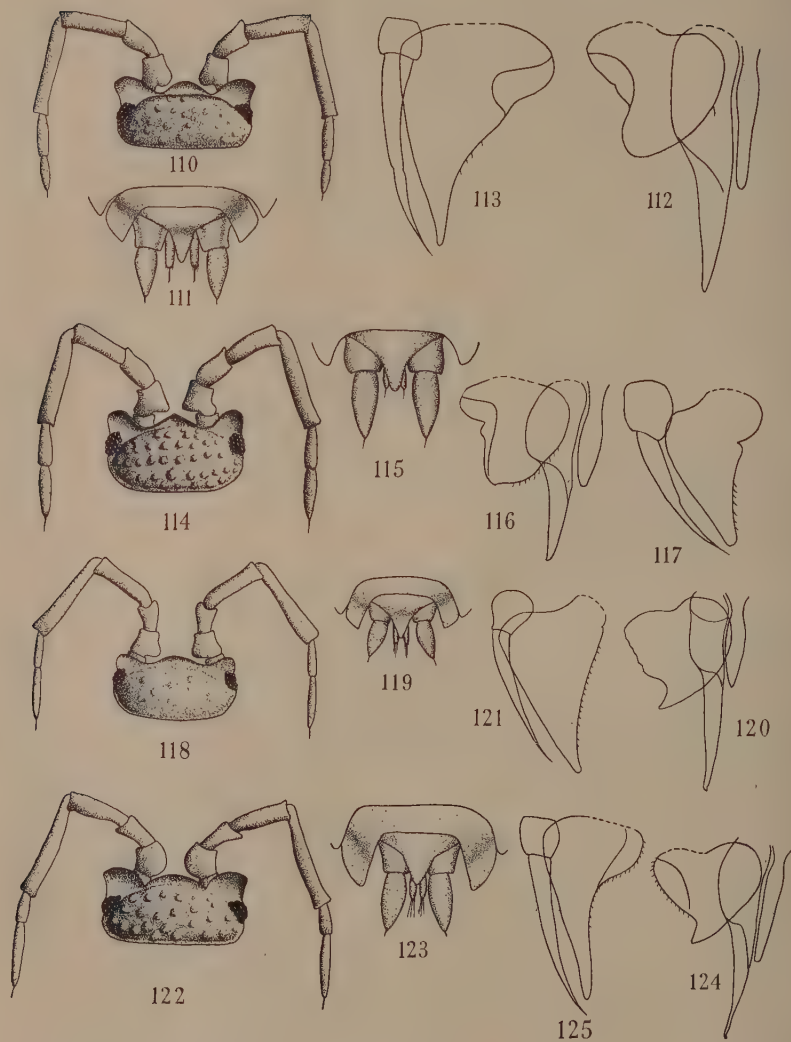
P. nemorensis Koch, 1839.

P. quercum Schnitzler, 1853.

Tracheoniscus ratzeburgi Verhoeff, 1917 b; nec *P. ratzeburgi* Dollfus, 1896.

Characters.

10.5 mm. long, nearly twice as long as wide. Colour grey, with a lighter strip down each side of the animal at the base of the epimera, the apices of the



FIGS. 110-113.—*Porcellio (Porcellio) spinicornis* Say. 110, head, $\times 13$; 111, telson and uropods, $\times 13$; 112, 1st δ pleopod and penis, $\times 20$; 113, 2nd δ pleopod, $\times 20$.
 FIGS. 114-117.—*Porcellio (Porcellio) scaber* Latreille. 114, head, $\times 13$; 115, telson and uropods, $\times 13$; 116, 1st δ pleopod and penis, $\times 20$; 117, 2nd δ pleopod, $\times 20$.
 FIGS. 118-121.—*Porcellio (Tracheoniscus) rathkei* (Brandt). 118, head, $\times 13$; 119, telson and uropods, $\times 13$; 120, 1st δ pleopod and penis, $\times 20$; 121, 2nd δ pleopod, $\times 20$.
 FIGS. 122-125.—*Porcellio (Tracheoniscus) ratzeburgi* (Brandt). 122, head, $\times 13$; 123, telson and uropods, $\times 13$; 124, 1st δ pleopod and penis, $\times 20$; 125, 2nd δ pleopod, $\times 20$.

latter also lighter. Antennae minutely scaled, the last peduncular segment five times as long as wide and approximately the same length as the flagellum; the distal segment of the latter twice as long as the proximal—a ratio which differentiates this from all other British species (fig. 122). Dorsum of the head and body somewhat feebly and irregularly tuberculate, the tubercles becoming restricted to a transverse area on the middle of the more posterior tergites, together with a row along the posterior margin. Frontal lobe wide, its anterior margin nearly straight in the middle, meeting the lateral lobes in a sharp, V-shaped incision each side; the lateral lobes strong, their lateral margins feebly angulate. Pseudotracheae on all five pairs of pleopods, the tubes feebly branched. Telson triangularly produced in the middle, the apex rounded. Exopodites of the uropods nearly three times as long as wide, depressed and lanceolate, the endopodites very nearly as long as the exopodites, reaching far beyond the tip of the telson, feebly compressed laterally, five times as long as wide. 1st and 2nd male pleopods as in figs. 124 and 125.

Distribution.

The species has been recorded from several English counties, from Somerset to Cumberland; from Dumbarton and the Orkneys in Scotland, Pembroke and Glamorgan in Wales. It has not as yet been recorded from Ireland.

Family **Armadillidiidae** Stebbing, 1893.

Vandel (1944), in a useful study on the head of the *Armadillidiidae*, has drawn attention to the significance of the sculpture of the anterior margin. There is, in this family, a strong, often triangular, sclerite at the top of the face, whose upper margin projects more or less above the anterior margin of the head, though it is sometimes bent backwards slightly over the head (see Diagram 2). This is known as the frontal lobe or *scutellum*. The upper margin

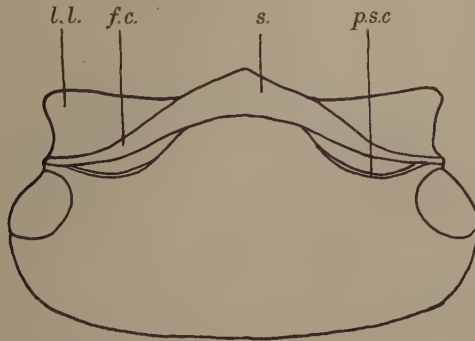


DIAGRAM 2.—Head of *Armadillidium pulchellum* (Zencker) from above: *f.c.*, lateral extension of frontal carina; *l.l.*, lateral lobe; *p.s.c.*, postscutellar carina; *s.*, upper margin of frontal lobe or scutellum (=median part of frontal carina).

of this scutellum is homologous with the frontal carina of *Porcellio*, and in *Eluma* it is continued on each side, as far as the sides of the head, as the lateral parts of the frontal carina. In *Armadillidium* however, it appears that the lateral regions of the frontal carina have undergone regression to a variable extent, and at the same time another carina, posterior to the first, has developed. This is the postscutellar carina of Vandel. In species such as *vulgare* and *nasatum* the lateral parts of the true frontal carina have completely

or almost completely (respectively) disappeared ; in others, such as *pictum*, a distinct frontal carina remains. The best example of this intermediate stage in the British fauna is *pulchellum* where the two carinae are present and the postscutellar carina is rather weaker than the frontal (fig. 136).

Characters.

Body strongly convex, integument usually smooth ; capable of rolling into a ball. Frontal lobe or scutellum of the head very strongly developed. Frontal and postscutellar carinae present either singly or together. Antennae short, the flagellum of two segments. Anterior margin of the endopodite of the maxilliped non-ciliated, with a small number of stout, dentiform processes. Epimera well developed but not expanded laterally at all, those of the 1st segment strongly produced anteriorly as far as the anterior margin of the head. Outline of the pleon continuous with that of the pereion. Uropods short, not projecting beyond the telson, their endopodites greatly expanded laterally so that they and the telson form a convex covering round the posterior end of the animal, continuous laterally with the epimera ; the endopodites slightly expanded, usually completely hidden from above by the telson (figs. 127, 128, etc.). Legs rather short, 1st two pairs of pleopods with pseudotracheae. Male genitalia not very different from those of the Oniscidae, though the endopodites of the 1st pair are often strongly divergent posteriorly, or the tips are bent outwards (figs. 134 and 135).

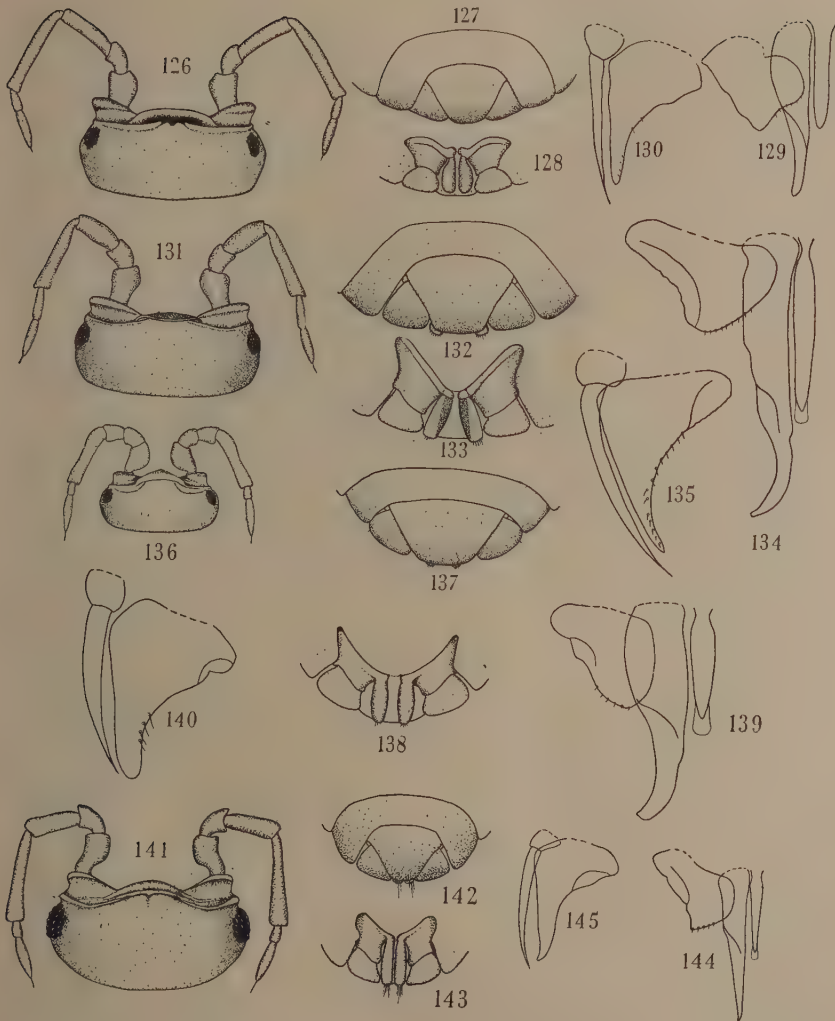
Genus ARMADILLIDIUM Brandt, 1833.

Characters.

Eyes compound. The upper margin of the frontal lobe (or scutellum) not continuous with the lateral or 'post-scutellar' carinae. Lateral margins of the 1st epimeron lacking a carina and furrow except in *opacum* where the groove is morphologically underneath the lateral margin of the epimeron. The remaining characters of generic significance are common to the two British genera, *Armadillidium* and *Eluma*, and have been included in the characters of the family.

Key to the species of Armadillidium.

- | | |
|--|------------------------------|
| 1. Exopodites of the uropods distinctly wider apically than long (the length measured close to the lateral margin (figs. 128, 133) | 2. |
| 2. Length of the exopodites of the uropods equal to or greater than their width (figs. 153, 158) | 6. |
| 2. Epimera of the 1st tergite with a groove along the inner (morphologically under) side of their lateral margins | <i>opacum</i> (Koch). |
| 3. Epimera without such a groove | 3. |
| 3. Proximal segment of the flagellum more than twice as long as wide (fig. 131) ; larger animals up to 18 mm. long | <i>vulgare</i> (Latreille). |
| 4. Proximal segment of the flagellum less than twice as long as wide ; smaller animals not more than 7 mm. long | 4. |
| 4. Sides of the telson straight or feebly convex ; distal segment of the flagellum at least four times as long as the proximal (fig. 136) | <i>pulchellum</i> (Zencker). |
| 5. Sides of the telson feebly concave ; distal segment of the flagellum less than four times as long as the proximal | 5. |
| 5. Postero-lateral angle of the exopodite of the 1st male pleopods rectangular, the endopodite straight (fig. 144) | <i>pictum</i> Brandt. |
| 6. That angle rounded, the endopodites slightly divergent for the posterior half of their length (fig. 149) | <i>album</i> Dollfus. |
| 6. Very large animals, up to 20 mm. long ; scutellum at least half as wide as the head measured to the ends of the post-scutellar carinae, the latter nearly straight (fig. 151) | <i>depressum</i> Brandt. |
| 7. Smaller animals, normally less than 10 mm. long, the scutellum less than one-third as wide as the head, the postscutellar carinae strongly arcuate (fig. 156) | <i>nasatum</i> Budde-Lund. |



FIGS. 126-130.—*Armidillidium opacum* (Koch). 126, head, $\times 13$; 127, telson and uropods from above, $\times 13$; 128, same from below, $\times 13$; 129, 1st δ pleopod and penis, $\times 20$; 130, 2nd δ pleopod, $\times 20$.
 FIGS. 131-135.—*Armadillidium vulgare* (Latreille). 131, head, $\times 13$; 132, telson and uropods, from above, $\times 13$; 133, same from below, $\times 13$; 134, 1st δ pleopod and penis, $\times 20$; 135, 2nd δ pleopod, $\times 20$.
 FIGS. 136-140.—*Armidillidium pulchellum* (Zencker). 136, head, $\times 13$; 137, telson and uropods from above, $\times 13$; 138, same from below, $\times 13$; 139, 1st δ pleopod and penis, $\times 28$; 140, 2nd δ pleopod, $\times 28$.
 FIGS. 141-145.—*Armadillidium pictum* Brandt. 141, head, $\times 28$; 142, telson and uropods from above, $\times 20$; 143, same from below, $\times 13$; 144, 1st δ pleopod and penis, $\times 20$; 145, 2nd δ pleopod, $\times 20$.

Armadillidium opacum (Koch), 1835. (Figs. 126–130.)*Armadillo opacus* Koch, 1835.*Armadillidium conspersum* Zaddach, 1884.*A. sulcatum* Budde-Lund, 1885; *nec* Milne-Edwards, 1840.*Characters.*

A medium sized species, up to 10 mm. long, twice as long as wide. The upper surface of the head very feebly and shallowly tuberculate. Colour, light grey, with irregular darker patches. Antennae slim, the last peduncular segment six times as long as wide and up to one-quarter as long again as the flagellum, the proximal segment of the latter only two-thirds as long as the distal. Upper margin of the frontal lobe or scutellum five-twelfths as wide as the head measured to the lateral extremities of the postscutellar carinae. The upper margin of the scutellum inclining forwards to a greater extent than in other species and thereby exposing the anterior margin of the head proper, which is seen to have a strong emargination in the middle flanked by two rounded processes. The upper margin of the scutellum is continued on each side as a distinct carina (the lateral part of the frontal carina) which runs to the lateral margin of the head and joins the postscutellar carina near the margin. The lateral margins of the epimera of the 1st tergite are thickened on the inside and hollowed out to form a groove for the reception of the antennae when the animal is rolled. This groove is similar in function to that of *Eluma*, but the latter is external to the margin of the epimera. Telson truncate apically, the corners rounded, four-thirds as wide behind as long in the middle; exopodites of the uropods truncate apically, one-third wider apically than long, the endopodites also wider than in most species, only twice as long as wide, their apices truncate.

Distribution.

It is doubtful whether this species occurs in Great Britain. Collinge (1941) claimed to have identified two specimens from Dorset, captured in 1917, but he was later unable to trace them. I have seen no British material of this species; nevertheless, it is described and figured in case it should later prove to occur here.

Armadillidium vulgare (Latreille), 1804. (Figs. 131–135.)*Armadillo vulgaris* Latreille, 1804.*A. variegatus* Latreille, 1804.*A. pillularis* Say, 1818.*A. ater* Schnitzler, 1853.*Armadillidium commutatum* Brandt & Ratzeburg, 1830–4.*A. zenckeri* Brandt, 1833.*A. trivialis* Koch, 1839.*Characters.*

This is the common 'Pill Bug'. Up to 18 mm. long, a little more than twice as long as wide. Colour, very varied, from completely black to pale yellow; the more usual varieties are light grey with paler longitudinal markings.* Antennae minutely spinulose, the last peduncular segment six times as long as wide and about one-fifth as long again as the flagellum; the latter of two segments, the distal usually longer than the proximal. When seen from in front, the upper margin of the scutellum is rather less than half as wide as the head measured to the ends of the postscutellar carinae. The latter not continuous with the scutellum. Lateral parts of the frontal carinae absent.

* For information on the genetics of colour varieties in this species see Howard (1940 and 1942).

Dorsum of the body smooth (under high magnification very finely punctulate). Telson truncate apically, the corners rounded, its width at the base nearly half as great again as its length in the middle. Exopodites of the uropods one-quarter to one-third wider than long. The apical third of the endopodites of the 1st male pleopods strongly divergent posteriorly (see figs. 134 and 135).

Distribution.

This species is widely distributed throughout the British Isles, and is particularly abundant on calcareous soils.

Armadillidium pulchellum (Zencker), 1799. (Figs. 136–140.)

Oniscus pulchellus Zencker, Koch in Panzer, 1799.

Armadillo maculatus Sill, 1861.

Armadillidium pictus Plateau, 1870; *nec* Brandt, 1833.

Characters.

A small species, 3.5 mm. long, twice as long as wide. Colour, dark brown with five irregular longitudinal areas paler, the width of the darker and paler areas variable; the head dark, usually with a paler macula in the middle near the posterior margin. Upper surface of the body smooth, minutely punctulate and spinulose under high power. Antennae rather short, the last peduncular segment four times as long as wide and about one-fifth as long again as the flagellum, whose distal segment is two to three times as long as the proximal. Scutellum of the head shallow compared with that of *vulgare*, rather more than half as wide as the head measured to the ends of the postscutellar carinae; the latter very feeble, and lying behind a better developed frontal carina, which is continuous with the upper margin of the scutellum. Telson truncate but somewhat rounded apically, one and a half times as wide behind as long in the middle, the exopodites of the uropods up to one-third as wide as long. Endopodites of the 1st male pleopods rather wide apically and strongly divergent (figs. 139 and 140).

Distribution.

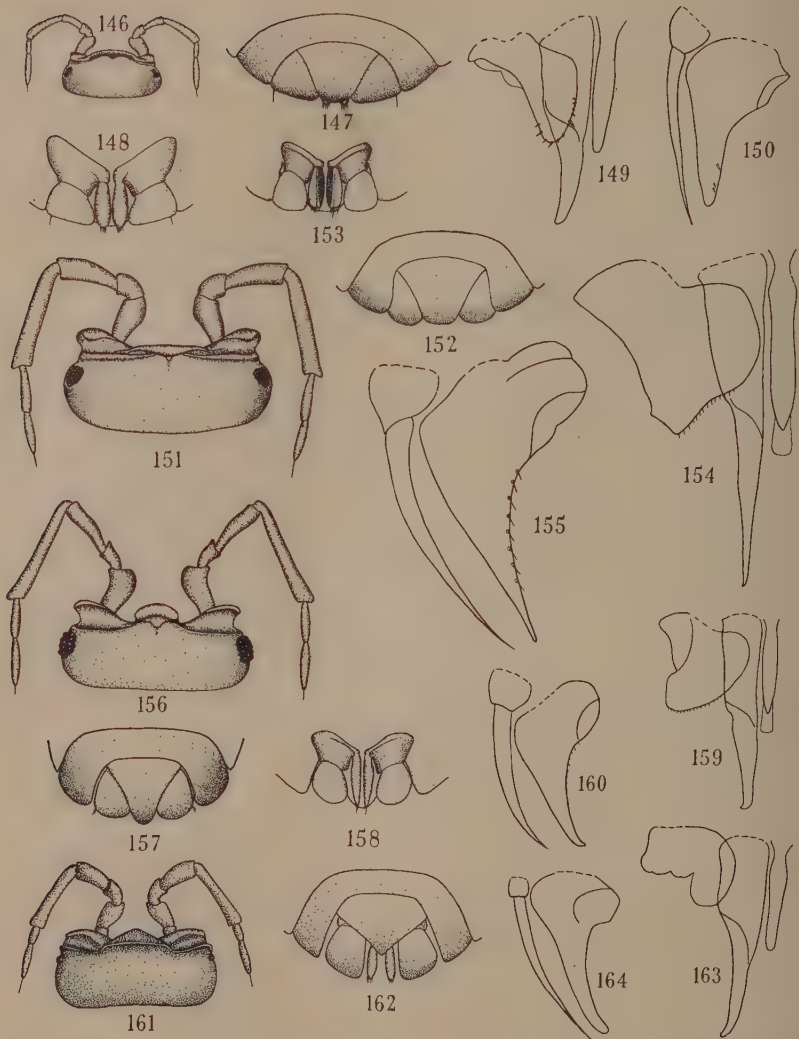
Recorded from several counties from Devon to Cumberland; from Radnor in Wales and from a few counties, both coastal and inland, in Ireland.

Armadillidium pictum Brandt, 1833. (Figs. 141–145.)

Armadillidium grubei Zaddach, 1844.

Characters.

A small species, up to 7 mm. long, about twice as long as wide. Colour various, often dark greyish brown with three rows of lighter maculae on the tergites, and a lighter band along each lateral margin of the body. Antennae rather short, last peduncular segment five times as long as wide and up to one-third as long again as the flagellum, whose distal segment is one and a half times to twice as long as the proximal. Upper margin of the scutellum nearly straight behind, five-ninths as wide as the head measured to the ends of the postscutellar carinae. A very feeble frontal carina present, continuous with the upper margin of the scutellum, running in front of the postscutellar carina and joining it before it reaches the margin of the head. Telson triangular, the apex rounded, nearly one-third wider behind than long in the middle; exopodites of the uropods nearly as long as wide. Endopodites of the 1st male pleopods long, their terminal portions not divergent behind except at the tips (fig. 144).



FIGS. 146-150.—*Armadillidium album* Dollfus. 146, head, $\times 13$; 147, telson and uropods from above, $\times 20$; 148, same from below, $\times 20$; 149, 1st δ pleopod and penis, $\times 20$; 150, 2nd δ pleopod, $\times 20$.
 FIGS. 151-155.—*Armadillidium depressum* Brandt. 151, head, $\times 13$; 152, telson and uropods from above, $\times 13$; 153, same from below, $\times 20$; 154, 1st δ pleopod and penis, $\times 20$; 155, 2nd δ pleopod, $\times 20$.
 FIGS. 156-160.—*Armadillidium nasatum* Budde-Lund. 156, head, $\times 13$; 157, telson and uropods from above, $\times 13$; 158, same from below, $\times 13$; 159, 1st δ pleopod and penis, $\times 15$; 160, 2nd δ pleopod, $\times 15$.
 FIGS. 161-164.—*Eluma purpurascens* Budde-Lund. 161, head, $\times 13$; 162, telson and uropods, $\times 13$; 163, 1st δ pleopod and penis, $\times 20$; 164, 2nd δ pleopod, $\times 20$.

Distribution.

The species is recorded from Devon to Westmorland, and from Carnarvon in Wales.

Armadillidium album Dollfus, 1887. (Figs. 146–150.)

Armadillidium album Bagnall, 1908 b.

Characters.

A small species, 6.0 mm. long, twice as long as wide. Colour, according to Dollfus, uniform white, but some of the British examples according to Bagnall have, in life, "the segments of the mesosome partially shaded with grey". The dorsal surface distinctly though sparsely spinulose. Antennae slim, the last peduncular segment five times as long as wide, and as long as the flagellum; the proximal segment of the latter only one-third (according to Bagnall less than one-third) as long as the distal. Scutellum wide, nearly three-fifths as wide as the head measured to the extremities of the postscutellar carinae, broadly rounded in front and curved somewhat forwards, exposing the anterior margin of the head, which has a wide, shallow emargination in the middle. The scutellum is continued on each side as a distinct frontal carina, which runs nearly to the margin of the head, the postscutellar carinae also present. In British material the frontal carina is relatively weaker and the postscutellar stronger. Telson three-sevenths wider behind than long in the middle, broadly rounded apically. Exopodites of the uropods only three-fifths as long as wide apically, their lateral corners each with a distinct spine; the endopodites also broader than in many species, two and a half times as long as wide in the middle. 1st and 2nd male pleopods as in figs. 149 and 150.

Distribution.

The species has, so far as I am aware, been recorded only once from England, under debris on the sands at the Taw estuary, Devon.

Armadillidium depressum Brandt, 1833. (Figs. 151–155.)

Characters.

Large animals up to 20 mm. long, twice as long as wide. Colour usually slaty grey with lighter markings, but sometimes the whole animal much lighter. The head rather more strongly transverse than in other species, 2.2 times as wide as long. Sometimes very feebly and shallowly tuberculate. Antennae with the last peduncular segment six times as long as wide, and one-fifth as long again as the flagellum, the distal segment of the latter one-fifth as long again as the proximal. Scutellum well developed and somewhat recurved above, its upper margin continued into very feeble frontal carinae, the latter not reaching as far as the sides of the head. Postscutellar carinae strong, the scutellum about half as wide as the head. Telson triangular, the apex rounded, one-seventh wider behind than long in the middle; exopodites of the uropods as long as wide or a little longer. All the male genitalia save the 1st exopodites strongly elongated, the 1st endopodites long and narrow, not divergent except at the tips (figs. 154 and 155).

Distribution.

Recorded from a few counties from the Channel Isles to Westmorland, but not from Scotland, Wales or Ireland,

Armadillidium nasatum Budde-Lund, 1885. (Figs. 156-160.)

Armadillidium speyeri Jackson, 1923.

Characters.

Up to 10 mm. long, about twice as long as wide. Colour greyish brown with darker markings often arranged in four longitudinal rows, the head dark, marbled with lighter markings. Antennae rather long and thin, the last peduncular segment eight to ten times as long as wide and about one-third as long again as the flagellum, the two segments of the latter equal in length. This species is not so strongly convex as *vulgare*, in particular the sides of the pleon make a smaller angle with the horizontal plane; associated with this slight difference in shape is the fact that the animal does not roll into a perfect sphere, and when rolled its antennae are left exposed. Frontal lobe or scutellum very strong, extending at right angles to the surface of the head, narrow, only one-third as wide as the head measured to the extremities of the postscutellar carinae; the sides of the scutellum at right angles to its upper margin, and continuous laterally for a short distance as feeble frontal carinae. Surface of the animal smooth, the margins of the epimera minutely toothed owing to the presence of numerous imbricate scales. Telson rather longer and narrower than in most species, one-fifth wider behind than long in the middle, the apex gently rounded, the sides distinctly concave. Exopodites of the uropods distinctly longer than wide, paddle-shaped, the endopodites comparatively long and narrow, five times as long as wide. In the male genitalia, the tips of both the 1st endopodites and the 2nd exopodites are curved outwards (figs. 159 and 160).

Distribution.

Recorded from Devon to Westmorland in England; Fife and Kinross in Scotland; Carnarvon and Pembroke in Wales; Antrim, Down and Wexford in Ireland.

Genus *ELUMA* Budde-Lund, 1885.

Eluma Budde-Lund, 1879, *nom nud.*

Characters.

Integument covered with a short pile of hairs. Scutellum or frontal lobe not so well developed as in *Armadillidium*, its apical margin continuous on each side with a frontal carina which runs to the antero-lateral corner of the head. Eyes each of one large ocellus. The outer surface of the epimera of the 1st pereionite bears a shallow groove running along the lateral margin, which serves to receive the antennae when the animal is rolled; the postero-lateral corners of these epimera notched. Telson not reaching the apex of the uropods, and leaving the endopodites exposed (fig. 162).

Eluma purpurascens Budde-Lund, 1885. (Figs. 161-164.)

Characters.

Up to 9.0 mm. long, rather more than twice as long as wide. Strongly convex. Colour purplish brown, with lighter longitudinal markings, particularly on the sides of the tergites. The whole surface bearing a pile of fine hairs, about 0.1-0.05 mm. long. Antennae rather short, the last peduncular segment five times as long as wide, and about one-quarter as long again as the flagellum; the latter of two segments, the proximal one only half as long as the distal. Scutellum triangular from in front, its upper margin very feebly rounded anteriorly; laterally, the upper margin continuous

with the strong frontal carina on each side. Telson triangular, the apex acutely rounded; its length equal to five-eighths of the width at the base, the apex short of the tips of the uropods by a distance equal to about half its total length. Exopodites of the uropods broadly expanded, their width approximately equal to their length; the endopodites much narrower, three and a half times as long as wide in the middle. In the male genitalia, the 1st exopodites are strongly emarginate several times on their posterior margins, the endopodites are feebly divergent for the apical third of their length and bent outwards at the tips; the 2nd exopodites have a very long, narrow apical region becoming narrower much nearer the base than is general in the family (figs. 163 and 164).

Distribution.

Recorded in the British Isles only from the Hill of Howth and Portmarnock, both in County Dublin, Ireland. The species is well known from the Atlantic coasts of Europe.

APPENDIX 1.

The following table lists the names used in the present monograph compared with the names by which the same species were previously commonly known to British authors. Where no change has been made, the name is recorded centrally in the table.

NEW NAME.	OLD NAME.
Ligiidae.	
<i>Ligia oceanica</i> (Linné).	
<i>Ligidium hypnorum</i> (Cuvier).	
Trichoniscidae.	
<i>Trichoniscoides albidus</i> (Budde-Lund).	
<i>Trichoniscoides sarsi</i> Patience.	
(<i>Species incerta.</i>)	<i>Trichoniscoides scabrous</i> Collinge.
<i>Trichoniscus pusillus</i> Brandt.	<i>Trichoniscus pusillus</i> Brandt.
<i>Trichoniscus pusillus provisorius</i> Racovitza.	<i>Trichoniscus pusillus</i> Brandt.
	<i>Trichoniscus pygmaeus</i> Sars.
<i>Cordioniscus stebbingi</i> (Patience).	<i>Trichoniscus stebbingi</i> Patience.
<i>Cordioniscus spinosus</i> (Patience).	<i>Trichoniscus spinosus</i> Patience.
<i>Androniscus dentiger</i> Verhoeff.	<i>Trichoniscus roseus</i> Koch.
<i>Androniscus weberi</i> Verhoeff.	<i>Trichoniscus roseus</i> Koch.
<i>Miktoniscus linearis</i> (Patience).	<i>Trichoniscus linearis</i> Patience.
<i>Oritoniscus flavus</i> (Budde-Lund).	<i>Trichoniscus vividus auctorum</i> (<i>nec</i> Koch).
	and <i>Trichoniscus vandeli</i> Collinge.
	<i>Haplophthalmus mengii</i> (Zaddach).
	<i>Haplophthalmus danicus</i> Budde-Lund.
Oniscidae.	
	<i>Philoscia muscorum</i> (Scopoli).
<i>Halophiloscia couchii</i> (Kinahan).	<i>Philoscia couchii</i> Kinahan.
<i>Chaetophiloscia patiencei</i> (Bagnall).	<i>Philoscia patiencei</i> Bagnall.
	<i>Platyarthrus hoffmannseggii</i> Brandt.
	<i>Oniscus asellus</i> Linné.
Porcellionidae.	
	<i>Cylisticus convexus</i> (De Geer).
<i>Metoponorthus pruinosis</i> (Brandt).	<i>Porcellionides pruinosis</i> Brandt.
<i>Metoponorthus cingendus</i> (Kinahan).	<i>Porcellionides cingendus</i> (Kinahan).
<i>Metoponorthus melanurus</i> Budde-Lund.	<i>Porcellionides melanurus</i> (Budde-Lund).
<i>Porcellio</i> (<i>Porcellio</i>) <i>scaber</i> Latreille.	<i>Porcellio scaber</i> Latreille.
<i>Porcellio</i> (<i>Porcellio</i>) <i>laevis</i> Latreille.	<i>Porcellio laevis</i> Latreille.
<i>Porcellio</i> (<i>Porcellio</i>) <i>spiniornis</i> Say.	<i>Porcellio spiniornis</i> Say.
<i>Porcellio</i> (<i>Porcellio</i>) <i>dilatatus</i> Brandt.	<i>Porcellio dilatatus</i> Brandt.
<i>Porcellio</i> (<i>Tracheoniscus</i>) <i>rathkei</i> (Brandt).	<i>Porcellio rathkei</i> Brandt.
<i>Porcellio</i> (<i>Tracheoniscus</i>) <i>ratzeburgi</i> (Brandt).	<i>Porcellio ratzeburgi</i> Brandt.

Armadillidiidae.*Armadillidium opacum* (Koch).*Armadillidium vulgare* (Latreille).*Armadillidium pulchellum* (Zencker).*Armadillidium pictum* Brandt.*Armadillidium album* Dollfus.*Armadillidium depressum* Brandt.*Armadillidium nasatum* Budde-Lund. *Armadillidium speyeri* Jackson.*Eluma purpurascens* Budde-Lund.

APPENDIX 2.

List of varieties not recognized in the main section of this monograph. The author is Collinge unless another is named.

Ligia oceanica var. *flavescens*, 1916.*Trichoniscus pusillus* var. *intermedius*, 1916.*Androniscus dentiger* var. *flavus*, 1916.*Oritoniscus flavus* var. *perlata*, 1946.*Haplophthalmus danicus* var. *armenius*, 1918; *bagnalli*, 1946; *nigrescens*, 1942; *virescens*, 1918.*H. mengii* var. *flavovirescens*, 1917.*Philoscia muscorum* var. *albescens*, 1918; *aureomaculatus* (sic), 1918; *maculata*, 1918; *nacrum*, 1916; *standeni*, 1917; *virescens*, 1917.*Oniscus asellus* var. *albidus*, 1916; *bicolor*, 1917; *flavescens*, 1917; *flavobrunneus*, 1917; *rufoflavescens*, 1918.*Metoponorthus pruinosis* var. *flavobrunneus*, 1917.*Platyarthrus hoffmannseggii* var. *flavobrunneus*, 1917; *prolongus*, 1941.*Cylisticus convexus* var. *brunneus*, 1917; *patiencei*, 1916.*Porcellio dilatatus* var. *flavus*, 1917; *rufobrunneus*, 1918.*P. laevis* var. *flavovirescens*, 1917; *maculatus*, 1917.*P. spinicornis* var. *aureomaculatus*, 1916.*P. scaber* var. *flavomaculatus*, 1918; *flavobrunneus*, 1917; *lateritius*, 1916 (nom. nov. for *rufa* Bagnall, 1909, nec Scott, 1893); *marmorata* Brandt, 1908; *rufa* Scott, 1893; *rufescens*, 1913.*P. (Tracheoniscus) rathkei* var. *birksei*, 1918.*Armadillidium depressum* var. *nigra*, 1943.*A. nasatum* var. *flavum*, 1918; *nigrescens*, 1918; *rufescens*, 1943.*A. pulchellum* var. *flavum*, 1917.*A. vulgare* var. *aureolineatum*, 1917; *bicolor*, 1917; *brunneoflavescens*, 1916; *brunneum*, 1942; *cooperi*, 1917; *flavescens*, 1944; *marginatum*, 1917; *nigrum*, 1948; *patoni*, 1942; *perlatum*, 1947; *quicksi*, 1946; *rufobrunneum*, 1918; *tesselatum*, 1917; *virescens*, 1917.

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